REVUE SUISSE DE ZOOLOGIE

ANNALES

de la
SOCIÉTÉ SUISSE DE ZOOLOGIE
et du
MUSÉUM D'HISTOIRE NATURELLE
de la Ville de Genève

Volume hors série II

Proceedings of the
XIIIth International Congress of Arachnology
Geneva, 3-8 September 1995
(ed. Volker Mahnert)

XIII
INTERNATIONAL
CONGRESS OF
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4-9 SEPTEMBER 1995
GENEVA-SWITZERLAND

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Purification and comparison of two toxic peptides (CSTX-1 and CSTX-2) in the venom of *Cupiennius salei* (Ctenidae)

Lucia KUHN-NENTWIG & Heinz MALLI
Zoological Institute, University of Berne
Baltzerstr. 3, CH-3012 Berne, Switzerland.

Purification and comparison of two toxic peptides (CSTX-1 and CSTX-2) in the venom of *Cupiennius salei* **(Ctenidae). -** It is proposed that CSTX-1 (a 74 amino acid toxin) is similar to CSTX-2 (a 61 amino acid toxin)and that the remaining 13 amino acids (mainly lysine) cause its much higher toxicity.

Key-words: Spider venom - peptid toxins - amino acid sequence.

Thirteen toxic peptides were obtained from the venom of the spider *Cupiennius salei* after a complex separation procedure by HPLC. The purity of the isolated peptides was controlled by SDS-PAGE. These peptides differ remarkably in concentration and molecular size (between 2,500 and12,000 Da) and represent different types of toxins. Only 5 toxins (CSTX-1, 4, 8, 9 and 13) have higher concentrations than 4 mg/ml venom (KUHN-NENTWIG *et al.* 1994).

The toxins also differ in toxicity. To quantify this, the *Protophormia* biotest was used, where the test substance is injected into blowflies (*Protophormia* spec., Calliphoridae, adults, 1 day old). Remarkable differences in toxicity covering a range of more than a factor of one hundred were measured. The most potent toxin is CSTX-1 and it represents 18 % of the total venom protein.

CSTX-1 consists of 74 amino acids and has a molecular mass of 8,352.6 Da. The 8 cysteines form 4 disulfide bridges and are responsible for the tertiary structure of the protein. Actually, nothing is known about the bridge arrangement between the cysteines. Experiments to determine this arrangement by treatment with trypsin (HECK *et al.* 1994) failed in the case of CSTX-1. Generally, the structure of most spider peptide toxins are defined by their dominant structural feature of disulfide linkages which cause that these molecules are conformationally bound and thereby partially protected from proteolytic activity (SACCOMANO *et al.* 1994).

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```
                +       -  -               -  +                 +  +
                                  10                                20
Ser-Cys-Ile-Pro-Lys-His-Glu-Glu-Cys-Thr-Asn-Asp-Lys-His-Asn-Cys-Cys-Arg-Lys-Gly-

        +       +                           -   -   -                   -
                                    30                                 40
Leu-Phe-Lys-Leu-Lys-Cys-Gln-Cys-Ser-Thr-Phe-Asp-Asp-Glu-Ser-Gly-Gln-Pro-Thr-Glu-

+                   +                            -                          +
                                    50                               60
Arg-Cys-Ala-Cys-Gly-Arg-Pro-Met-Gly-His-Gln-Ala-Ile-Glu-Thr-Gly-Leu-Asn-Ile-Phe-Arg-

            +       +   +   +       +   +       +
                                70
Gly-Leu-Phe-Lys-Gly-Lys-Lys-Lys-Asn-Lys-Lys-Thr-Lys
```

FIG. 1

Charge distribution in the amino acid sequence of CSTX-1.

Unusual in CSTX-1 are 7 lysines among the last 10 amino acids. A search in a data bank for protein sequence data showed that until now no protein with such an unusual sequence had been found. This lysine rich tail is also responsable for the distribution of the charges within the molecule so that a strongly positive section results, presumably important for the binding process at its target structure (Fig. 1). It is possible, that the toxicity of CSTX-1 is caused by or correlated to this lysine rich part. However, this could not be proved, because experiments to cut of this end by treatment with proteases such as carboxypeptidase P failed.

By checking 9 independent lines of monoclonal antibodies against CSTX-1 (Malli et al. in prep.) the obtained antibodies showed an additional specificity against CSTX-2 as shown in an immunoblot (Fig.2).The amino acid analysis and the theoretical calculation of the CSTX-2 show a high similarity with CSTX-1 when the last 13 amino acids are omitted (Tab.1). So we could estimate the molecular mass of CSTX-2 with 6,865.75 Da. Investigations by mass spectrometry (Fig. 3) confirmed this calculation with an estimated molecular mass of 6,864.5 Da and showed, that the molecular masses of CSTX-1 (minus the last 13 amino acids) and CSTX-2 are identical. A first amino acid sequence analysis with non-reduced and non-alkylated CSTX-2 could be performed until position 10. So far, it is identical with CSTX-1, two gaps in the sequence probably indicate the position of 2 cysteines (Fig.4).

We now conclude, that CSTX-2 is a shorter form of CSTX-1. Since CSTX-1 (LD50 0.41 µg/ fly) is 20 times more toxic than CSTX-2 (LD50 8.16 µg/fly) there is strong evidence, that the toxicity of CSTX-1 is mainly caused by its lysine rich

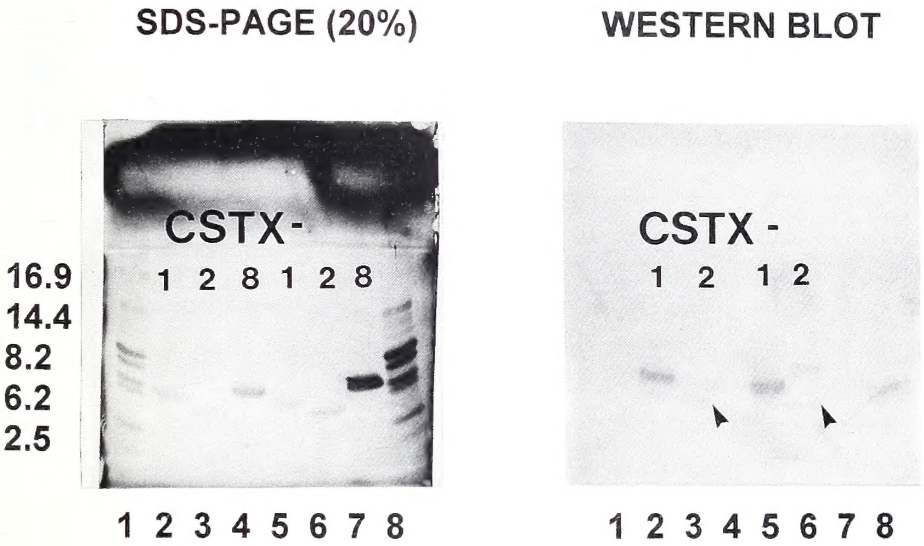

FIG. 2

Western blot analysis of CSTX-1 and CSTX-2.At the left side SDS-PAGE (20 % acrylamide, silver stained) of CSTX-1 (lane 2 & 5), CSTX-2 (lane 3 & 6) and CSTX-8 (lane 4 & 7). The concentrations of the probes are 4 µg for CSTX-1 & 2 and for CSTX-8 6 µg (lane 4) and 8 µg (lane 8). Lane 1 and 8 are molecular mass markers (2.5-17 kDa) (Pharmacia). At the right side is the immunoblot (Cellulosenitrate, 0.2 mm) of this SDS-PAGE with a monoclonal antibody against CSTX-1. Staining is caused by peroxidase-conjugated, goat anti-mouse immunoglobulins.

TAB. 1
Amino acid analyses of CSTX-2

AS	theoretical	M/M	(+/-)
ASP/ASN	6	6.2	0.2
GLU/GLN	8	8.6	0.6
SER	3	2.6	-0.4
GLY	5	5.3	0.3
HIS	3	3.4	0.4
ARG	4	4.2	0.2
THR	4	3.8	-0.2
ALA	2	2.1	0.1
PRO	3	3.1	0.1
TYR	0	0.1	0.1
VAL	0	0.1	0.1
MET	1	1	0
CYS	8	6.8	-1.2
ILE	3	2.8	-0.2
LEU	3	3.3	0.3
PHE	3	2.9	-0.1
LYS	5	5.4	0.4
TOTAL	61	61.7	0.7

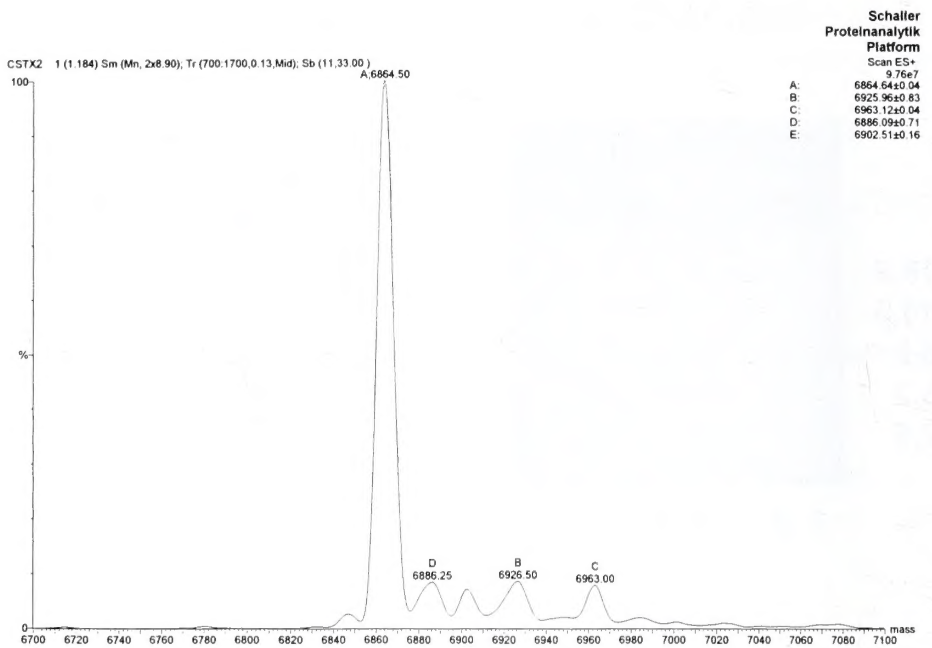

FIG. 3

Mass spectrometry (electrospray-MS) of CSTX-2 (5 pMol/µl).

CSTX-1 Ser-Cys-Ile-Pro-Lys-His-Glu-Glu-Cys-Thr-Asn-.....

CSTX-2 Ser-XXX-Ile-Pro-Lys-His-Glu-Glu-XXX-Thr

FIG. 4

Comparison of the N-terminal amino acid sequence of CSTX-1 (reduced and alkylated) and CSTX-2 (non-reduced).

carboxyl end. This could mean, that a positively charged domain is responsible for the binding to a target structure such as ion channels in the cell membranes of neurons.This is supposed by REILY *et al.* (1995) for ω-Aga-IVB, a toxic peptide from the spider *Agelenopsis aperta*. However, we do not know, whether such a shorter form of a toxin is the result of a degradation process induced by proteases or really reflects two independent toxins.

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Variation in egg production of *Pityohyphantes phrygianus* (C.L. Koch) (Linyphiidae, Aranaeae), influenced by temperature and latitude

Gary H. P. LÅNG
Section of Animal Ecology, Department of Zoology, Göteborg University, Medicinaregatan 18, S - 413 90 Göteborg, Sweden.

Variation in egg production of *Pityohyphantes phrygianus* (C.L. Koch) (Linyphiidae, Aranaeae), influenced by temperature and latitude. - The effects of temperature and geographic origin on the production of eggs and egg sacs of female *Pityohyphantes phrygianus* (C. L. Koch) were examined in a laboratory experiment. Subadults of three populations, 160 - 800 km apart, were sampled and the spiders were raised to maturity and mated. The females were then kept at 10°, 15° and 20°C, respectively. The egg sacs were removed from the cages and the egg mass was weighed. Females reared at the highest temperature produced, on average, twice as many egg sacs, had a 50% reduction of the reproductive life span and put 50% less egg mass in each egg sac compared to females reared at the lowest temperature. In spite of these differences, the total mass of eggs produced was similar for all temperatures and populations except for the females of the northernmost population in the highest temperature (20°C). The females of this group on average died earlier when reared at the highest temperature and could not produce more egg sacs than in lower temperatures. This suggests that genetic or prereproductive environmental factors affect the plasticity of the female reproduction.

Key-words: egg production-temperature-environmental factor-reproduction.

INTRODUCTION

The spider *Pityohyphantes phrygianus* (C. L. Koch) is widespread in boreal areas in Scandinavia. When different populations of the same species occur in areas with large environmental differences such as different average ambient temperature or seasonal length, one can expect that a reaction norm exists for traits important to fitness. A reaction norm is the phenotypic or plastic response of a genotype along an environmental gradient (STEARNS 1989). Differences between populations in their

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plastic response to environmental factors may be due to genetic constraints, preventing the development of an optimal response for all environments (THOMPSON 1991).

The effect of temperature and geographic origin on the following population parameters has been tested in a laboratory experiment: Number of egg sacs produced, egg mass per egg sac, total mass of eggs, time until first oviposition and total reproductive lifespan.

MATERIAL AND METHODS

I collected subadult ♂♂ and ♀♀ of the sheet-web spider *P. phrygianus* in March and April 1993 from three populations in forests of spruce (*Picea abies*); **A)** Härskogen, 30 km east of Göteborg (UTM: 64 03 80, 3 24 150); **B)** Snapen, 10 km north of Mariestad (UTM: 65 11 25, 4 34 400 and **C)** Vassnäs, 110 km west of Östersund (UTM: 70 51 20, 4 02 200). The spiders were reared to maturity in 500 ml plastic jars under constant laboratory conditions. The temperature was kept at 20°C and each spider was supplied with equal amounts of food (about 10 flies/week), *i.e.* vestigial-winged fruit flies (*Drosophila melanogaster*). This feeding regime was kept throughout the experiment. After maturity the ♀♀ were randomly paired with one male from the same population when enough males were available. In seven cases for population **A** and three cases for population **C**, males from population **B** had to be used instead of males from populations **A** and **C**, respectively. When the male populations of origin were used in the Kruskal-Wallis test, the number of eggs produced showed no correlation with the male origin, so male populations were left out in the final analysis. The ♀♀ were then assigned to three different temperatures, 10°C, 15°C and 20°C in which they were kept until they died. The jars were checked every other day and egg sacs were removed, to count and weigh the eggs. In about 10 % of the clutches the eggs were "glued" together and could not be counted. No differences were found in the average mass per egg from different clutches in those clutches that could be counted. I therefore used egg mass as a measure of egg production. Twelve spiders (22,2 %) that did not produce any egg sacs before death were not included in the analysis.

All data were analysed with Kruskal-Wallis non-parametric ANOVA for three or more groups using StatView 4.02 for Macintosh. All p-values given are from this test. To determine which groups being significantly different, I used the method of multiple comparisons between treatments in the Kruskal-Wallis test (SIEGEL & CASTELLAN 1988).

RESULTS

When the populations were pooled the egg mass per egg sac decreased with increasing temperature ($p=0,0147$). When the populations were tested separately, however, none of the populations showed a significant decrease (fig 1), probably due to the low sample size. The average egg mass/egg sac in population **A** decreased from

6,9 mg at 10°C to 3,4 mg at 20° (p=0,1141) and in population **C** from 11,0 mg at 10°C to 5,0 mg at 20°C (p=0,0804). In population **B** the average egg mass/eggsac were more similar between temperatures, ranging from 4,6 mg at 10°C to 3,1 mg at 20°C (p=0,3229). No significant differences were found between populations, even when temperatures were pooled (p=0,1487).

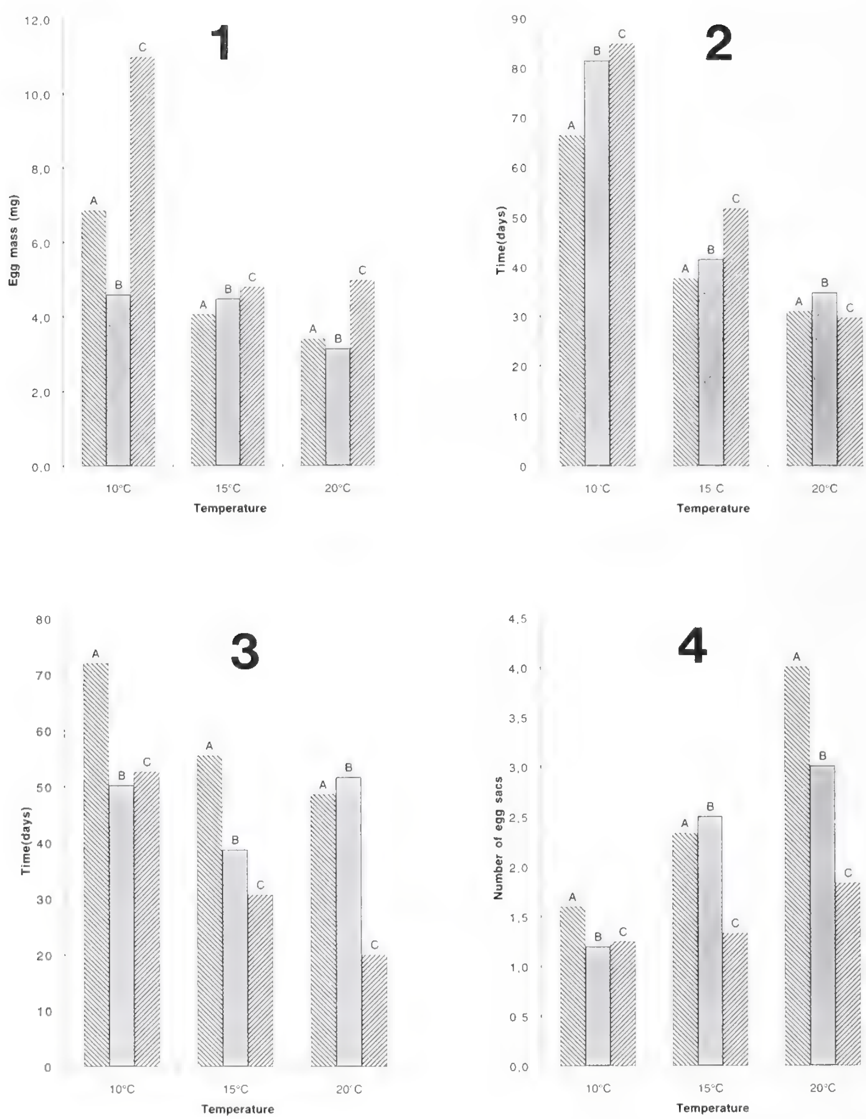
The average time from the start of the experiment to first reproduction (i.e. production of first egg sac) decreased significantly with increasing temperature (fig.2) for all populations. In population **A** the average time decreased from 66,4 days in 10°C to 31,0 days in 20°C (p=0,0024). In population **B** from 81,4 days in 10°C to 34,8 days in 20°C (p=0,0079) and in population **C** from 84,8 days in 10°C to 29,7 days in 20°C(p=0,0264).

The ♀♀ of the northern population **C** seemed to suffer disproportionately from high temperature, since they had a shorter average reproductive lifespan (fig.3) in 20°C (20,0 days) than in 10°C (52,7 days), while ♀♀ of the two other populations seemed unaffected by temperature. Population **C** had a significantly shorter reproductive lifespan compared to the other populations when temperature groups were pooled (p=0.0191). But this difference between populations is not consistent across the temperature interval. The reproductive lifespan of the population **C** at 20°C was significantly shorter than for the other populations (p=0.0149). It was also shorter, but not significantly so, at 15°C (p=0.1163), whereas at 10°C population **C** was intermediate between populations **A** and **B** and no significant differences in the reproductive lifespan could be observed (p=0.7216). As a result of this the ♀♀ of the northern population **C** produce fewer clutches in 20°C than populations **A** and **B** (P = 0.0198) whereas in lower temperatures the number of clutches do not differ between populations (fig.4).

DISCUSSION

The general results shown in this study can be interpreted as a behavioural reaction norm to differences in ambient temperature. *Pityohyphantes phrygianus* matures, mates and produce offspring in early spring and if the earliest developmental stages are sensitive to cold temperature, then ♀♀ should delay their oviposition as much as possible in low temperatures to ensure their progeny a better environment for development. On the other hand, when experiencing high temperatures, ♀♀ risk that it is late in the season so their progeny's development before winter becomes too short and therefore they should produce egg sacs as quickly as possible. The result of this study is qualitatively similar to the result in a study by Downes (1988) on *Theridion rufipes* Lucas. Downes concluded that at the temperature where no embryos developed, ♀♀ delayed their first oviposition and extended their oviposition intervals significantly.

Egg mass per egg sac also decreases with temperature, but this, I suggest, is depending on the decreasing time between ovipositions when temperature increases. It has previously been shown that for spiders clutch weight is linearly dependent on



FIGS 1-4

Fig. 1. Average eggmass per eggsac. Sample sizes: 10°C: **A** n=4, **B** n=4, **C** n=3; 15°C: **A** n=6, **B** n=6, **C** n=3; 20°C: **A** n=6, **B** n=5, **C** n=5. - Fig. 2. Average time from start of experiment to first reproduction. Sample sizes are the same as in figure 1. - Fig. 3. Average time from first egg production to death. Sample sizes are the same as in figure 1. - Fig. 4. Average number of egg sacs produced. Sample sizes are the same as in figure 1.

pre-laying weight of the female (HIGGINS 1992) and spider weight is linearly dependent on food consumption (KESSLER 1971; TURNBULL 1962).

The failure of the ♀♀ of the northern population to produce on equal amount of eggs in 20°C as they do in lower temperatures can not be explained within the pattern described above. Considering the shorter summer season and lower average temperatures experienced by spiders in northern populations, one might expect them to do better than the other populations in low temperatures and worse in high temperatures, but no significant differences in the ability to manage with low temperatures were discovered.

I conclude that there is a plastic response in the reproductive behaviour of the female *P. phrygianus* to variations in temperature and that higher temperature shortens the time between egg sacs, which leads to fewer eggs in each sac. I also conclude that ♀♀ from the northern population (**C**) died earlier at high temperatures, making it impossible to produce more egg sacs than in lower temperatures. There are at least two possible explanations for the pattern observed here, (i) genetic factors are controlling the plastic response and that northern and southern populations differ genetically, or (ii) the response may be triggered by environmental cues during juvenile growth.

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Origin of the Polynesian Spiders

Pekka T. LEHTINEN
Zoological Museum, University of Turku
20014 Turku, Finland

Origin of the Polynesian Spiders. - Endemic species comprise ca. 60% of 280 species of Polynesian spiders. The great majority of the East Polynesian endemic species are restricted to mountain-top forests above 800 m, while a part of the West Polynesian endemic species can be found in less spoiled lowland habitats. Contrary to previous opinions, the indigenous spider fauna of Polynesia has not come solely from the west. One-third of the endemic fauna has its closest relatives in South America and/or Hawaii, while only ca. 10 species have their origin in New Zealand or subantarctic areas. The strongest speciation concerns the groups of eastern origin, in Tetragnathidae, Theridiidae, Mysmenidae, Thomisidae, and Salticidae, with most of these comprising the first colonizers several million years ago from South America or Hawaii. In contrast, endemic groups with only 1–2 Polynesian species and apparently no significant speciation within Polynesia seem to have a western origin. Western Polynesia also has a much higher diversity of spider families, as 9 families or new groups are only present in western Polynesia and four families or isolated groups are present only in eastern Polynesia. Moreover, some families and subfamilies are indigenous in the western parts, but only anthropochorous in the eastern parts.

The anthropochorous spider fauna of Polynesia consists mainly of widespread species, but many Pacific species have extended their range by anthropochorous dispersal. The spider fauna of Easter Island only consists of anthropochorous species, with many of these having restricted range elsewhere.

The presence of spider genera without any close known relatives in the mountain tops of Polynesia could partly be explained by the island-chain theory. The island chains extending to Polynesia seem to be up to 43 million years old, although none of the recent islands are more than 9 million years in age.

Key-words: Polynesia - origin of species - endemism - eastern species - western species - southern species - cosmopolitan - anthropochorous

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INTRODUCTION

This is a short preliminary report of one aspect of "the Polynesia project", a large inventory and revisional program of the terrestrial arthropods of Polynesia, coordinated by myself and largely based on recent field work of the author in 1988–95. Among the zoogeographical issues this report will focus solely on the origin of the Polynesian spider fauna.

This report is based on a parallel taxonomic revision of all families of Polynesian spiders which has been completed for ca. more than half of the families. Nevertheless, all families have been sufficiently investigated to enable a general discussion of different origins. A large body of mainly unpublished material from neighbouring areas (Melanesia, southeast Asia, Australia, New Zealand, Galapagos and Hawaiian islands and South America) has been investigated for classification of the origins of Polynesian spiders.

Several different definitions of Polynesia have been proposed, sometimes including Fiji, Hawaii, and New Zealand. However, here Polynesia will be delimited more strictly, following the practice usual in zoogeographical discussions. This Polynesia (Fig. 1) includes the archipelagoes extending from the Easter Island to the Tonga Islands and in the north from the Line Islands to the Austral Islands.

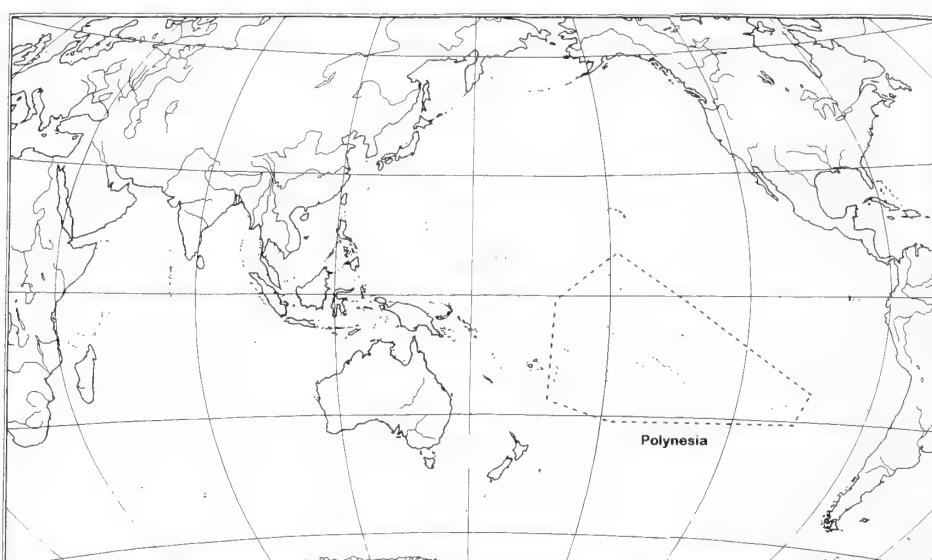

FIG. 1

The Pacific with the delimitation of Polynesia

In the early days of zoogeography Polynesia was simply treated as a subregion of the large Indo-Pacific or Australian regions, though this classification was based solely on the terrestrial vertebrate fauna, which is quite poor in all remote archipelagoes of the Pacific. Although many of the early studies have focused on describing the most frequent Polynesian spiders (KOCH & KEYSERLING 1871–86, KARSCH 1881, RAINBOW 1897, POCOCK 1898, KULCZYŃSKI 1911, STRAND 1911, 1913, 1915, and ROEWER 1944), none of these authors have speculated on the origins of these spider species due to lack of sufficient information from surrounding areas.

Most discussions on the zoogeography of the Polynesian spiders are derived from taxonomic and faunistic papers published either by BERLAND (1924*a*, 1929, 1939, 1934*a*, 1935*a*, 1938*a*,*b*, 1942) or by MARPLES (1951, 1955a,b, 1957, 1959, 1964). BERLAND (1924*b*, 1930, 1938*a*) discussed also the Polynesian fauna in papers dealing with New Caledonia, New Zealand, and New Hebrides and also published several purely zoogeographical reviews (BERLAND 1928, 1934*b*,*c*, 1935*b*, 1937). Although both of these authors presented hypotheses concerning the origin of the spider fauna of the Pacific archipelagoes, much of their material was incorrectly assigned at the generic, tribal, or subfamily levels, or was even incorrectly identified. Moreover, much of that material consisted of samples from cultural habitats.

In addition to these papers, even recent work by BERRY & BEATTY (1987) has assumed that the whole Polynesian spider fauna of natural habitats would have originated from the west, Melanesia, southeast Asia or Australia. A part of the fauna was classified as cosmopolitan, but no clearcut distinction was made between anthropochorous and indigenous species by either Berland or Marples.

Scattered new information of the spiders from adjacent Pacific islands has subsequently been presented in many minor papers by various authors (FORSTER 1959, SUMAN 1965, 1967, 1970, GERTSCH 1973, BRIGNOLI 1973, 1976, 1980, LEHTINEN & SAARISTO 1980, LEHTINEN 1981, 1982, OPELL 1983, BEATTY & BERRY 1988*a*,*b*. The spider fauna of New Zealand has been described in six volumes of a handbook, as well as in several group revisions by Forster and his coworkers. General problems in determining the arachnological biogeography of the Pacific have since been discussed by FORSTER (1975), FORSTER & PLATNICK (1977), LEGENDRE (1978), BERRY & BEATTY (1987), BEATTY *et al.* (1991) and also by myself in several revisional papers and in two preliminary zoogeographical reports (LEHTINEN 1980, 1993). The endemic fauna and speciation processes of some Polynesian endemic groups of spiders in Hawaii have also been recently studied by SUMAN (1970), GILLESPIE (1991, 1992, 1993, 1994), GILLESPIE & CROOM (1992), and GILLESPIE *et al.* (1994), while the results of recent studies of the fauna of the Galapagos Islands has been reported in several papers by a Belgian team (BAERT & MAELFAIT 1986; group revisions). Unpublished material of the present author from the Galapagos and Hawaiian Islands adds important data for the study of Polynesian spiders of South American and Hawaiian origin. BAERT & JOCQUE (1993) compared the zoogeography of spiders in several oceanic islands, but their data from the Marquesas Islands and Easter Island was restricted to the old papers of BERLAND (1924, 1933, 1935*a*) and the

percentages given by them for endemic, cosmopolitan and continental species must now be revised.

Since the syntheses of BERLAND and MARPLES, the spider fauna of all areas surrounding Polynesia have been actively studied by many specialists, including myself. Essential new information, both published and unpublished is now available from Southeastern, Eastern and Southern Asia, Chile, New Zealand, Melanesia, Micronesia, Australia, and the subantarctic islands.

Most of the collecting before the Polynesia-project was done with traditional methods (hand picking, sweep netting, etc.). Different habitats also seem to have been quite unevenly studied, and in many groups the majority of specimens in museums are anthropochorous species from villages or from within their vicinity. Given these limitations, it is not surprising that the general zoogeographical conclusions drawn from such data might be widely erroneous, or at best only partly correct.

The last twenty years of general biogeography have been characterized by a rise in entirely new theoretic approaches based on or parallel to the simultaneous evolution of new hypotheses and findings from geophysics, biological systematics and paleontology, as well as the development of easily applicable computer techniques.

WILSON (1963) concluded that the present geology of the Pacific archipelagoes had resulted from continental drift. The most detailed hypotheses about the history and geological evolution of the Polynesian and Hawaiian seamount-island chains have been presented by MORGAN (1972) and DALRYMPLE *et al.* (1973). They hypothesized that the age of the northwestern parts of these chains is much higher than that of the more recent islands at the southeastern end, and that the Hawaiian chain would be more than 40 million years old and not 1–6 million years as has been generally accepted for the larger islands of the Hawaiian chain (MCDOUGALL 1964).

If MORGAN'S (1972) hypothesis of the age and pattern of evolution for the Polynesian island chains were valid, it would also imply that there has been a continuous chain of closely spaced islands both from the northwestern part of the Line Islands through northern French Polynesia and the Gambier Islands to Easter Island as well as another chain from the Marshall and Ellice Islands to the Austral Island chain. However, this geological theory would involve volcanic activity occurring on the ocean bottom, but it would not demonstrate that all parts of such a chain (islands and seamounts) would have ever risen above the surface. Such a view posits a continuum of island chains over a period of 30–50 million years, sufficient for the evolution of very specialized endemic biota, but it would not explain much about the origins of this evolution — except that the oldest islands in the chain are the most northwestern.

Some parts of the oceanic ridges are known to have moved along tranverse fracture zones. Easter Island lies on one of these segments and its present exceptionally long distance from the other islands of the Tuamotu–Gambier islands can be explained by this phenomenon. Unfortunately, most of the endemic arthropod species of the forest soil of Easter Island obviously became extinct in prehistorical time with the destruction of the forests by the Polynesians. Possible remnants of this interesting fauna still await study. Most Easter Island spiders consist of widespread species found around the villages and in the vegetation of open habitats.

It is thus clear that previous conclusions on the origin of Polynesian spiders have been prejudiced due to inadequate collecting in natural habitats, as well as incorrect generic assignment of the majority of species.

POLYNESIAN SPIDER FAUNA

My personal field work for the Polynesia-project has revealed at least 280 species of spiders representing 36 traditional families (44 revised families) in Polynesia, of which ca. 62% are endemic. Nearly 22% of the species are also found in neighbouring parts of Melanesia, Micronesia or South America. Some of these "regional species" have a wider range in the Indo-Pacific region or neighbouring parts of Australia, although they are indigenous to at least some parts of Polynesia. Forty-three species (16%) are mainly synantropic or at least their original dispersal to some Polynesian islands has been aided by man. Part of these are pantropical or even cosmopolitan, but some have obviously come directly from more remote areas (Europe, North America).

No indigenous species of Loxoscelidae, Oecobiidae, Titanoecidae, and Zodariidae are found in Polynesia, and the following worldwide families have not succeeded in entering Polynesia: Oxyopidae, Amaurobiidae, Ctenidae, Anapidae, Mimetidae, Trachelidae, and Deinopidae. A palpimanid species was recorded from Kiribati, very close to Polynesia, but it was originally described as *Oonops triangulipes* (Karsch, 1881). Among the well represented families, some dominant worldwide subfamilies are lacking in Polynesia, as Theridiidae: Euryopinae, Zodariidae: Storeninae and Corinnidae: Castianeirinae. In addition to these, no indigenous species of Uloboridae: Uloborinae are present.

Many Gondwanian groups, which are rich in species in neighbouring areas, are also apparently absent in Polynesia, especially Orsolobidae, Stiphidiidae, Psechridae, Micropholcommatidae, Archaeidae, Cycloctenidae, and Stenochilidae.

A large number of the species discussed here belong either to undescribed genera or should be transferred to other genera. No new generic or familial names are used here, though in some cases the most usual binominal combination has been replaced by a previously published, but much less widely used, taxonomically correct combination, marked by an asterisk *. The limitation used for many genera differs widely from those used by Berland, Marples, or other authors dealing with Polynesian fauna. New synonyms are not listed here, while some groups are treated simply by referring to the close relationship between genera. In order to allow interpretation of some details of the results, it has been necessary to publish here a few other taxonomic acts, e.g., the transfer of *Nukuhiva* from Pisauridae to Lycosidae, the transfer of *Chiracanthium* to Micrommatidae Järvi, 1914 and the transfer of *Oonops triangulipes* from Oonopidae to Palpimanidae. The original type designation of the Oonopid genus *Xestaspis* Simon, 1884 (*Oonops loricatus* L. Koch, 1872) is also noted here.

Theridiidae s.lat. includes Hadrotarsidae; Linyphiidae s.lat. also includes Erigonidae, Mynoglenidae and a new group; Oonopidae s.lat. includes all groups of the classical Oonopidae except Orsolobidae; Clubionidae s.lat. includes Micrommatidae, but no other groups of the classical Clubionidae.

TABLE 1

Polynesian spider families

end = N of endemic species; reg = N of regional species; syn = N of synanthropic species; ? = N of sp. of uncertain origin

	N	end	reg	syn	?
Theridiidae s.lat.	49	33	7	8	1
Salticidae	38	19	12	5	2
Tetragnathidae	31	20	8	2	1
Linyphiidae s.lat.	22	12	5	2	3
Oonopidae s.lat.	21	10	6	3	2
Araneidae	17	8	7	2	
Mysmenidae	12	11	1	–	
Pholcidae	9	3	1	4	1
Uloboridae	7	5	1	1	
Thomisidae	7	6	1	–	
Desidae	6	4	2	–	
Clubionidae s.lat.	6	5	–	1	
Scytodidae	5	1	2	2	
Hahniidae	5	5	–	–	
Lycosidae	5	3	2	–	
Gnaphosidae	5	2	–	3	
Ochyroceratidae	4	2	–	1	1
Dictynidae	3	2	–	–	1
Anyphaenidae	3	2	1	–	
Corinnidae	3	1	1	1	
Tetrablemmidae	2	2	–	–	
Heteropodidae	2	1	–	1	
Theridiosomatidae	2	1	1	–	
Symphytognathidae	2	2	–	–	
Loxoscelidae	2	–	–	2	
Oecobiidae	2	–	–	2	
Araneoidae ? family	1	1	–	–	
Barychelidae	1	1	–	–	
Filistatidae	1	1	–	–	
Cryptothelidae	1	1	–	–	
Segestriidae	1	1	–	–	
Dolomedidae	1	1	–	–	
Titanoecidae	1	–	1	–	
Agelenidae	1	–	–	1	
Zodariidae	1	–	–	1	
Nesticidae	1	–	–	1	
[Palpimanidae	1		not included]		
36	280	166	59	43	12
all species % of	280	59.3	21.1	15.4	4.3
? excluded % of	268	61.9	22.0	16.0	–

SPECIATION AND THE ORIGIN OF THE ENDEMIC SPECIES

The endemic species are now strongly concentrated in natural mountain habitats at elevations of over 800 meters in French Polynesia and the highest parts (250 – > 800 m) of the islands in western Polynesia. Among the species-rich families (5 spp. or more), the richest in endemic species are comprised of Hahniidae (100%)

and Mysmenidae (92%), the poorest Scytodidae (20%, but for ssp. 60%), Pholcidae (33%), followed by Araneidae and Oonopidae (47%). No endemic species have been documented on Easter Island. Lowland endemics in eastern Polynesia are restricted to a few intertidal or coastal species (*Paratheuma*, *Arangina*, "*Lycosa*"), while several others are present in the more natural habitats of western Polynesia. Two widepread species have invaded the natural habitats of mountain tops by aeronautic dispersal (*Eidmannella pallida* & *Erigone prominens*).

The phylogenetic relationships of the genera of several families are imperfectly known in South America, East and Southeast Asia and Hawaii. For many families, even the limits of the genera have not been established. Therefore, the exact origin could not be confirmed for a part of the Polynesian spider fauna. Two-thirds of these certainly have additional range or closest relatives in Melanesia, southeast Asia or northeastern Australia (western species).

Several Polynesian spider genera have no known close relatives. Two new Polynesian groups of Araneoidea s.lat. seem to originate from southeast Asia, while the enigmatic Marquesan genus *Uapou* is quite isolated.

The majority of species with eastern origin live in the mountainous islands of French Polynesia, while the species with southern origin are only exceptionally (*Paro simoni*) confined to Rapa Island and many of these are found even in the Marquesas Islands.

1. Eastern species

One-third could be termed "eastern species", with 16% having South American affinities and an additional 12–13% most probably originating from South America via the Hawaiian or Galapagos islands. The largest group of South American origin consists of the theridid tribe Anelosimini (*Cyllognatha* & some undescribed genera) with ca. 10 endemic species, all anyphaenids, and most ochyroceratids (*Ceruleocera* & unplaced species). Three groups with strong Polynesian speciation also have parallel speciation in the Hawaiian islands: *Mecaphesa* (Thomisidae) (LEHTINEN 1993), Hawaiian "*Tetragnatha*" (GILLESPIE 1991, 1992, 1993, 1994) and the Hawaiian Salticid group related to *Bianor*.

The Oonopid species of the Pacific region are poorly known, but at least *Triaeris lepus*, "*Oonopinus*" *kilikus*, and "*Scaphiella*" *ula* (SUMAN 1965) are present both in Hawaii and Polynesia and seem to have their relatives in the Neotropical region. The only endemic scytodid species of Polynesia has all its relatives in Central America, Galapagos Islands, and Eastern Micronesia, with the mysmenid genus *Tamasesia* probably having also a similar range. The two corticicolous Polynesian gnaphosid species have not yet been assigned to genera, but their affinities (*Sergiolus* and *Herpyllus*) suggest an eastern origin.

Many pantropical anthropochorous species (e.g. *Physocyclus globosus*, "*Scytodes*" *fusca*, and "*S.*" *longipes*, and *Ostearius melanopygius*) are of South American origin, and at least *Frigga crocuta*, *Dendryphantes mordax*, **Tarapaca concinna*, and *Loxosceles laeta* have spread directly from there to Polynesia.

Three families, Anyphaenidae (endemic *Australaena* & an unidentified South American species), Segestriidae (unplaced "*Ariadna*" without males), and Mynoglenidae (all undescribed spp.), as well as the enigmatic *Uapou maculata* have not been found in western Polynesia. Representatives of "*Ariadna*" s.lat. are present in Melanesia and the Philippines, though the Polynesian species seem to be more closely related to Neotropical groups of this unrevised group.

2. Southern species

The eleven indigenous southern species (< 5%) have their closest relatives in New Zealand or in the subantarctic islands. Most of them belong to Linyphiidae s.lat. (*Paro*, *Maorineta*, four undescribed Mynoglenidae), but the coastal dictynid genus *Arangina* from New Zealand also has Polynesian species. A new theridid genus from Polynesian mountain tops is related to *Armigera* from the islands outside New Zealand. Five originally European and North American species among the anthopochorously spread species have probably dispersed to Eastern Polynesia (mainly Easter Island) through southern South America or New Zealand.

Most species shared by Polynesia and Australia are either widespread or synanthropic in either of these regions (*Gea heptagon*, *Eriophora transmarina*).

3. Pacific species

Two coastal groups of spiders with numerous endemic species are found in the Pacific. The genus *Paratheuma* (alternatively listed in Desidae and Dictynidae) resides in intertidal habitats and has extended its range into Japan (YAGINUMA 1990), the Caribbean region and the coast of Mexico (BEATTY & BERRY 1988*a*,*b*). The unrevised lycosid genus, including "*Lycosa tongatabuensis*" and several related species is found in open coastal habitats and also has a Pacific range, although not found in Central America. The mountain-top lycosid species *Nukuhiva adamsoni* is a more distant relative of this group, despite its originally being described (BERLAND 1933) and always catalogued as Pisauridae.

Non-coastal Pacific groups are represented by the deviating Uloborid genus Tangaroa, sometimes classified as a subfamily (LEHTINEN 1967). Endemic species of this genus have been reported in New Caledonia and Micronesia, but none have been found in the westernmost parts of the Pacific. Another, but still unnamed group, consists of several local endemics of Scytodidae ranging from Kalimantan to Micronesia, Polynesia, and the Galapagos islands. The Galapagos species has consistently been misidentified as "*Scytodes*" *hebraica*, but the holotype of the latter belongs to a strictly Neotropic, unnamed genus.

**Xestaspis loricata* (Oonopidae) is widespread in the archipelagoes of the central Pacific, and *Lucetia distincta* from Cuba is congeneric; *Xestaspis* is at least a valid subgenus of *Gamasomorpha*. Another genus of Oonopidae s.lat., a new genus related to *Orchestina* is only known from different parts of Polynesia, but may be more widespread.

Some large worldwide genera have undergone speciation within the Pacific, leading to species groups restricted to the Pacific region: Tetragnathidae: *Glenognatha* ("*Hivaoa*"), Araneidae: *Neoscona* (*maculatipes*-group), Theridiidae: *Argyrodes* (*unimaculatus*-group) and *Ariamnes*. The Pacific species of *Glenognatha* constitute the largest assemblage of Pacific endemic spiders. The species, originally assigned to *Hivaoa* and *Dyschiriognatha*, constitute a group of ca. 20 endemic species, but most *Hivaoa* spp. (BERLAND 1933, 1942) are not closely related to the type species of *Hivaoa*. *Hivaoa* was synonymized with *Glenognatha* by LEVI (1980), and a worldwide revision of its subgenera and species groups have not yet been completed.

The widespread orb-web spider *Neoscona theis* provides a good example of a pacific lowland or middle altitude species of a worldwide species group. Although it is found along the coasts of the Asian mainland, everywhere else in inland Asia this genus is represented by other species, while a close relative *Neoscona moreli* lives in the remaining tropical coasts and archipelagoes of Africa and the Caribbean.

"*Leucauge*" *granulata* is another instance of an orb-weaver with similar range. However, there are no close relatives in the Neotropical region, and this large Old World genus still lacks a valid name.

4. Western species

A large majority of Polynesian endemic species can be classified as western species, although there are no large species groups. In addition to the species discussed here, many species of unknown origin most probably have their closest relatives in Melanesia or southeast Asia.

First, it must be emphasized that six spider families with a wide range to the west of Polynesia are restricted to western Polynesia (Tonga & Samoa Islands, etc.): Tetrablemmidae (*Fallablemma* & *Tetrablemma*), Symphytognathidae (*Patu*), Theridiosomatidae (*Andasta* & "*Theridiosoma*", Cryptothelidae (*Cryptothele*), Dolomedidae ("*Dolomedes*"), Barychelidae (*Idioctis*), as well as some well-defined subdivisions of families as Tetragnathidae: Nephilinae (*Nephila*), Corinnidae: Oedignathinae (*Oedignatha*) and a group of Araneoidea s.lat. ("*Bathyphantes*" *paradoxus*) probably representing an undescribed family. In many cases, the Polynesian species is the easternmost one in a large Indo-Pacific or Old World genera (*Tetrablemma*, *Cryptothele*, *Oedignatha*).

Some genera with considerable speciation in Melanesia have extended their range into western Polynesia: *Artoria* (Lycosidae), *Daramulunia* (Uloboridae), *Ulesanis* and a new genus (Theridiidae), *Hirtia* and a new genus (Clubionidae) and *Bigois* (Hahniidae). The delimitation of many Melanesian Salticid genera is still unstable, though the Polynesian "genera" *Flacillula*, *Rarahu*, *Tatari*, and "*Pseudomaevia*" sensu BERLAND, 1942 are synonymous or closely related to more widespread, mainly Melanesian genera.

Numerous endemic species of quite uncertain origin have been recorded. Many of these are not discussed here, but some examples are offered to highlight the

deficiencies in our present knowledge. The type species of the deviating minute soil theridiid *Tekellina* has been reported from the Caribbean region, though a rather widespread undescribed species bas been found in western Polynesia and another undescribed species in India. An oonopid species is certainly found from two well-studied archipelagoes, the Seychelles and the Easter Island. The common western Polynesian dictynid of the vegetation layer, *Banaidja bifasciata*, and the predominant erigonid genus of the Marquesan mountain tops, *Uahuka*, have no known relatives. A minute slow-moving spider with unique feeding habits and gnathocoxal structure from Samoa may represent a new family in Araneoidea s.lat.

Baert & Jocque (1993) used the term "continental species" for a part of spider species of oceanic islands. They claimed that 22% of Easter Island species would be continental (Australian). However, there are no indigenous species left in Easter Island and no continental indigenous species in eastern Polynesia. Synanthropic species cannot be classified continental. The species of western Polynesia extending their range into continental Asia or Australia are all found in disturbed habitats and therefore more or less anthropochorous (e.g., "*Argyrodes*" *nigra*, *Ulesanis sextuberculata*, *Nephila plumipes*, *Tylorida striata*, *Andasta semiargentea*, *Tetragnatha demissa*) or belong to different subspecies (both *Dictis* spp).

ORIGIN OF THE NON-ENDEMIC INDIGENOUS SPECIES

This category includes numerous inaccuracies, as many groups have not been properly revised outside Polynesia. The whole picture is also confused by the fact that many "indigenous" species are not actually indigenous to all islands within their range but have been randomly aided by human activities.

Most species of this group consists of web spinning spiders of Araneoidea s.lat. They are widespread in the Southeast Asian archipelagoes, and many of these also live in the coastal areas of the Asian mainland: Araneidae: *Gea heptagon*, *Cyrtophora moluccensis*, *Anepsion rhomboides*, Tetragnathidae: *Tetragnatha demissa*, *T. macilenta*, *T. laqueata*, *T. protensa*, "*Leucauge*" *granulata*, *Tylorida striata*, *Nephila plumipes*, Theridiidae: "*Argyrodes*" *nigra*, Mysmenidae: *Mysmenella illectrix*, Theridiosomatidae: *Andasta semiargentea*, Linyphiidae: *Nesioneta pacificana*, Erigonidae: *Erigone bifurca*.

Spiders of other groups are represented by salticids (*Thorelliola ensifera*, *Athamas whitmaei*, **Zenodorus microphthalmus*, *Bavia aericeps*, **Ascyltus opulentus*, pholcids ("*Pholcus*" *ancoralis*, *Holocneminus piritarsis*) and some Oonopids (*Opopaea sauteri*, *O. lena*, "*Dysderina*" *insulana*) and scytodids (*Dictis tardigrada*, *D. striatipes*), as well as the only Pacific titanoecid *Pandava laminata*.

For many species, the known range is restricted to Melanesia and Polynesia only, as in *Efate albobicincta*, "*Flacillula*" *minuta*, and *Cytaea piscula* (Salticidae), "*Diaea*" *praetexta* (Thomisidae), *Chiracanthium mordax* (Clubionidae s.lat.), and the coastal lycosid, most often referred to as "*Lycosa tongatabuensis*".

ORIGIN OF THE ANTHROPOCHOROUS SPECIES

Many Polynesian anthropochorous species were absent from samples of BERLAND and MARPLES and some species were not classified as anthropochorous or were incorrectly identified. A few species which are usually classified as synanthropic also live in Polynesia as far as the most natural mountain tops (*Eidmannella pallida*). It has certainly spread to many uninhabited areas through aerial dispersal and thus is not always anthropochorous. Other widespread species with partly anthropochorous, partly aerial dispersal are the Linyphids *Microbathyphantes palmarius* and *Nesioneta pacificana*.

A. European — Mediterranean species have spread mainly to Easter Istand, but some of them have succeeded in becoming also established on tropical islands. Some species (**Stearodea grossa*) have obviously invaded Easter Island from South America, while the route for other species of this category remains unclear (Linyphiidae: *Lepthyphantes tenuis*, Pholcidae: *Pholcus phalangioides*, Oecobiidae: **Thalamia navus*, Loxoscelidae: *Loxosceles rufipes*, Gnaphosidae: *Trachyzelotes kulczynskii* and *Urozelotes rusticus*, Tetragnathidae: *Tetragnatha nitens*, and Agelenidae: *Tegenaria domestica*). The species comprising this category are mostly recent immigrants that have spread to Polynesia after the appearance of Europeans.

B. North American species. "*Coleosoma*" *adamsoni* (Theridiidae) seems to originate from the New World, most probably from North America, where several related species have been recorded. It is also present in a variety of natural habitats in Polynesia. *Zodarion trispinosum* has come to Hawaii and Polynesia from North America, but it may be an unrevised species of Palaearctic origin (cf. BAERT & JOCQUE 1993). In addition, two North American salticids are found on Easter Island.

C. Neotropical species. *Creugas cetratus* and *Meriola arcifera* (Corinnidae) as well as an unidentified species of Anyphaenidae, and *Selkirkiella* sp. (Theridiidae), **Tarapaca concinna* (Oecobiidae), and *Loxosceles laeta* (Loxoscelidae) certainly represent the anthropochorous fauna originating from South America. *Frigga crocuta* (Salticidae) has mostly spread anthropochorously, although it is also permanent inhabitant of lower mountain habitats.

D. Indo-Pacific species. In contrast to the species indigenous to parts of Polynesia, these species are characterized by a distinctly discontinuous Polynesian range, such as *Gasteracantha mammosa* and *Gea heptagon* (Araneidae) and *Odontodrassus javanus* (Gnaphosidae). The latter species has widely penetrated into natural habitats on the uninhabited Henderson Island (BENTON & LEHTINEN 1995). Some indigenous western Polynesian–Melanesian species have spread only anthropochorously to the eastern parts of Polynesia: *Cyrtophora moluccensis* (Araneidae) and "*Pritha*" *bakeri* (Filistatidae). *Chiracanthium mordax* ("Clubionidae") and *Pandava laminata* (Titanoecidae) may belong to either of these categories. *Eriophora transmarina* is also widespread in Australia, but its total range is obscure. Species of the genera *Erigone* and *Eperigone* are frequent aeronauts, and as such their exact colonization history is difficult to trace.

E. Species of the Old World tropics. *Neoscona vigilans* (Araneidae), **Parasteatoda mundula* (Theridiidae), *Microbathyphantes palmarius* (Linyphiidae) and *Opopaea punctata* (Oonopidae) are widespread in the Old World tropics, but seem to reach their eastern limit in Polynesia.

F. Pantropical species are mostly ancient introductions and their actual routes to Polynesia cannot be traced. Some of them are known to have their origin in the Neotropical region (Ochyroceratidae: **Theotima minutissima*, Oonopidae: *Heteroonops spinimanus*, Erigonidae: *Ostearius melanopygius*, Scytodidae: "*Scytodes*" *fusca*, "*S.*" *longipes*). Other pantropical species include: Uloboridae: *Zosis geniculatus*, Theridiidae: *Nesticodes rufipes*, **Parasteatoda tepidarioria*, *Coleosoma floridana*, Salticidae: *Menemerus bivittatus*, *Hasarius adansoni*, *Plexippus paykulli*, Heteropodidae: *Heteropoda venatoria*, Pholcidae: *Smeringopus elongatus*, *Artema mauriciana*, *Physocyclus globosus*. *Latrodectus geometricus* (Theridiidae) is very widespread in the Southern hemisphere, but has arrived in Easter Island from Chile.

It is interesting to note that two strictly synanthropic Pholcid species, *Artema mauriciana* and *Physocyclus globosus* have strongly declined since the Second World War. Their indoor habitats have probably been conquered by *Nesticodes rufipes*, *Zosis geniculatus*, and even the indigenous "*Pholcus*" *ancoralis*.

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The ultrastructure of leg skin in the phylogeny of spiders

Pekka T. LEHTINEN
Zoological Museum, University of Turku
SF-20014 Turku, Finland.

The ultrastructure of leg skin in the phylogeny of spiders. - The ultrastructure of the leg skin was studied with SEM in most spider families. The plesiomorphic leg skin type in labidognath spiders is ridged and is also predominant in most Amaurobiomorpha (RTA Clade + relatives). Ridged skin is correlated with the presence of several types of hairs, longitudinally ridged bothrial base, and in the majority of families (RTA Clade) also by the presence of tarsal trichobothria. Araneoidea s.lat. (= Araneomorpha *sensu* LEHTINEN 1978) is characterized by scaly skin correlated with a single, serrate type of leg hair, smooth bothrial base, and lack of tarsal trichobothria. Both skin types may be secondarily modified, but there are no known cases of reversal to the ridged type in Araneoidea s.lat. Scaly or ridged scaly types not homologous with the Araneoidean type have evolved in parallel in some groups not related to each other, but the phylogenetic position of the groups outside Araneoidea s.lat. is demonstrated by the presence of other, correlated synapomorphies of Amaurobiomorpha and some other groups (Mecysmaucheniidae, Drymusidae, Caponiidae). Some subfamilies or still unnamed infrafamilial groups in Zodariidae, Corinnidae, Caponiidae and Palpimanidae have modified leg skin, in spite of presence of ridged skin in other groups of the same family. Nicodaminae with scaly skin and Megadictyninae with smooth skin are probably not closely related. Papular skin is dominant in Thomisidae, but smooth in Nesticidae. Ultrastructural results in Uloboridae, Mimetidae, and Archaeoidea support some alternatives in the phylogenetic placement of these groups with disputed relationships. The evolution of the Mygalomorph skin type, as well as the the outgroups of the main subdivisions of the order Araneae remain unresolved.

Key-words: leg skin - ridged type - scaly type - ultrastructure - SEM.

INTRODUCTION

Phylogenetic analyses for the main groups of spiders have recently been carried out using computer programs with little or no methodological checking. The computer has been very effective in the time-consuming comparison of complex

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matrices, and most of the results are obviously correct. However, a number of problems can be seen to arise, when this method is used without sufficient critics. Some merely technical problems of cladistic analysis have been discussed in detail, e.g., the missing characters by PLATNICK *et al.* (1991 *b*) and comparison of the advantages and disadvantages of the most common programs (PLATNICK 1987, 1988). As emphasized by PLATNICK (1989 *b*: 21): "The open question, then, is not so much how best to analyze a data matrix, but how best to represent organismic variation in the matrix". More precisely, incorrect results appear to be mainly due to misinterpretations of homologies and polarities, erroneous coding and deficiencies or unbalanced selection of characters.

If a majority of characters analyzed are associated with a single adapation, a restricted complex of morphological and ethological characters, it is always theoretically possible to create a cladogram, where all taxa sharing this adaptation become "more related to each other than to other groups", independent of possible parallelisms in this adaptation. Accordingly, such an approach may omit or underrepresent characters of other, adaptively independent character complexes which may unite or separate taxa in entirely different ways.

The value of non-reversible single characters, e.g., the number of tarsal claws, is easily lost among the multitude of small reversible characters (details of genital structures) in computer programmes based on the principle of the most parsimonous tree. GRISWOLD (1993) used this principle without character weighting for the number of the tarsal claws and presented a cladogram of his "Lycosoidea" with numerous three-clawed groups "evolved" from two-clawed ancestors.

The ultrastructure of all chitinous surfaces includes a very large group of characters, the use of which has been quite restricted in most recent computer analyses of spiders. The leg skin of all labidognath spiders (= Araneomorpha s.lat.) is relatively monotonous, and only two basic types are present: ridged (Figs 1-2, 5-10) and scaly (Figs. 3-4, etc.). Some adaptive modifications are present in various families, mostly in spiders of dry habitats, but one of these two basic types is usually preserved in at least some details.

However, many of these characters are not correlated with other character groups or with behavioral adaptations, e.g., the numerous characters of the spinning organs that have predominated in most of these analyses.

The type of leg skin is very strongly correlated to the type and structure of unmodified hairs. The significance of these characters in spider phylogeny has been discussed by LEHTINEN (1967, 1971, 1975 *a*, *b*, 1976, 1978) and in Mygalomorphae by RAVEN (1985). A more reliable interpretation of modified leg skin types is made easier when other ultrastructural characters are analyzed together with those of the leg skin.

SEM micrographs of the leg skin of various spider families have often been unintentionally published in connection with depicted details of various leg structures, mostly the bothrial base or tarsal organ. Previous reports by this author (LEHTINEN & SAARISTO 1980, LEHTINEN 1981) have also included such data in written descriptions, but no interfamilial comparison was made, Useful SEM micrographs with or without

discussion of the findings have been published especially by Platnick's group working for AMNH: PLATNICK (1975, 1984 *a,b*, 1986, 1989 *a*, 1991, 1994 *a,b*), PLATNICK & LAU (1975), PLATNICK & GERTSCH (1976), GERTSCH & PLATNICK (1979, 1980), RAVEN & PLATNICK (1981), FORSTER & PLATNICK (1984), COYLE (1984), PLATNICK & GOLOBOFF (1985), FORSTER *et al.* (1987, 1990), GRISWOLD (1987, 1990, 1993), PLATNICK & FORSTER (1989, 1993), JOCQUE (1991, 1994), PLATNICK & GRIFFIN (1990), PLATNICK *et al.* (1991 *a*), PLATNICK & DI FRANCO (1992), PLATNICK & BRESCOVIT (1994), and OVTHSHARENKO *et al.* (1994). However, wide-scale phylogenetic discussions based on this character are rare. The tarsal organ and the base of the bothria have been separately depicted in numerous recent papers, though no author has yet attempted to make a phylogenetic analysis based on such a widely studied character. Furthermore, no author has even sought to include a sufficient number of ultrastructural characters for computer analysis, nor have these two skin types or their modifications been correctly coded (CODDINGTON *et al.* 1991).

In contrast, some ultrastructural characters with a narrow range in spiders have been analyzed in detail, e.g., the tibial glands of the Leptonetids by PLATNICK (1986) and specializations of the tarsal organ of Microstigmatidae by PLATNICK & FORSTER (1982). The ultrastructural characters of the carapace, chelicerae, and abdomen were widely discussed by LEHTINEN (1981) in Tetrablemmidae and many of them have been sporadically depicted in SEM micrographs by other authors without their use for wide-scale phylogenetic analysis of higher taxa.

The present report concentrates to the results of a screening of the leg skin ultrastructure of most spider families with the aid of SEM-micrographs. The polarity of evolution of this and some other ultrastructural characters is discussed, as well as the meaning of these results for the placement of several groups with disputed relationships.

MATERIAL

For the present synthesis, the ultrastructure of the leg skin was compared between most spider families, mostly based on the author's SEM-studies, with reference made in some cases to reliable published data (for details, cf. introduction). More than 600 SEM micrographs of the leg skin were taken in 1971-1995.

The term "ridged" has been previously used by CODDINGTON (1990). The basic type characterizing this pattern consists of parallel ridges separated by furrows and could as well be called "furrowed".

For problematic families, especially Mimetidae, Uloboridae, Deinopidae, Palpimanidae, Zodariidae, and Corinnidae, the types of leg hairs and setae, bothrial bases, onychial structures, tarsal organ and other sensory organs (when present) were also analyzed in detail.

RESULTS

A. Leg skin type of different spider families/genera

The dominance of the unmodified ridged type has been confirmed in the following families:

Mygalomorpha: Dipluridae (*Allothele*), Nemesiidae: Diplothelopsinae (*Mygaloides*), Barychelidae (*Encyocrypta*) (Fig. 6).

Primitive Cribellata: Austrochilidae (Fig. 5), Hypochilidae, Gradungulidae (fig. 7).

Haplogynae: Dysderoidea: Oonopidae s.lat., Orsolobidae, Segestriidae: Segestriinae; Scytodoidea: Ochyroceratidae, Telemidae, Leptonetidae; other haplogynae: Pholcidae, Caponiidae: Nopinae & Caponiinae (isolated family).

Palpimanoidea: Palpimanidae: Otiothopinae (Fig. 8).

Amaurobiomorpha: separate cribellate groups: Psechridae (Fig. 2); Dinopoidea: Dinopidae (Fig. 44), Uloboridae (Figs. 1, 41-43); Oecobioidea: Urocteidae, Hersiliidae (Fig. 11); Lycosoidea: Lycosidae, Ctenidae, Cycloctenidae (Fig. 36), Dolomedidae, Zoropsidae, Trechaleidae; unplaced: Tengellidae, Toxopinae, Miturginae (Figs. 10,34), Machadoniinae, Uliodoninae; Titanoecidae, Amaurobioidea: Amaurobiidae, Agelenidae, Anyphaenidae, Liocranidae, Zoridae (Fig. 9); Dictynoidea: Dictynidae, Hahniidae (Fig. 35), Desidae, Anyphaenidae; Pisauroidea: Pisauridae, Oxyopidae, Senoculidae; Clubionoidea: Clubionidae, Micrommatidae, Heteropodidae, Philodromidae, Trachelidae; Salticoidea: Salticidae (Fig. 12).

Ridged type with predominance of a smooth or anastomosing type:

Haplogynae: Scytodoidea: Scytodidae; unplaced haplogynae: Pholcidae, Diguetidae, Plectreuridae, Tetrablemmidae; Eresidae (Fig. 21) Amaurobiomorpha: Palpimanoidea: Palpimanidae, Stenochilidae; Gnaphosoidea: Gnaphosidae: Platorinae, Cithaeronidae, Prodidomidae, Trochanteriidae, Ammoxenidae; Zodarioidea: Zodariidae: Zodariinae (Fig. 19), Storenomorphinae, & Storeninae: *Cybaeodamus & Leprolochus* (Figs. 15,33), Cryptothelidae; Corinnoidea: Corinnidae: Corinninae (Fig. 20), Castianeirinae + several unplaced, ? family: Phrurolithinae.

Dominance of papular or smooth type:

Filistatidae (Fig. 18), Thomisoidea: Thomisidae: Thomisinae (Figs. 13,14,), Stephanopsinae, Stiphropinae, Homalonychidae (Fig. 22); Palpimanidae: *Palpimanus*; Megadictynidae (Fig. 46).

Scaly type and absence of ridged type has been checked in all families of Araneomorpha s.str.:

Araneoidea: Araneidae (Figs. 3,40), Metidae, Tetragnathidae, Anapidae, Symphytognathidae, Theridiosomatidae, Mysmenidae, Linyphiidae, Mynoglenidae, Erigonidae, Mimetidae (Figs. 37,39), Micropholcommatidae (Fig. 38), Theridioidea: Theridiidae, Hadrotarsidae, Synotaxidae, two new groups of possible family status, Archaeoidea: Archaeidae, Holarchaeidae.

Finely granular/smooth type:

Nesticidae (Fig. 17), Cyatholipidae.

The presence of various "scaly types" in combination with remnants of the ridged type or hair bases and hair types typical of Amaurobiomorpha:

Gnaphosoidea: Cithaeronidae (in some areas); Zodarioidea: Storeninae, Corinnidae (*Oedignatha*), Homalonychidae (Fig. 22), Nicodamoidea: Nicodamidae (Fig. 45).

Mygalomorph "scaly types":

Antrodiaetidae, Atypidae, Migidae, Ctenizidae, Idiopidae, Nemesiidae: Anaminae (*Aname*) (Fig. 32), Hexathelidae (Fig. 4), Paratropididae, Mecicobothriidae, Microstigmatidae.

Autapomorphic "scaly-papular" types (not related to each other):

Heptathelidae, Liphistiidae (Fig. 31), Microstigmatidae (*Ministigmata*), Microstigmatidae: Micromygalinae (*Micromygale*).

Mixed types (ridged scales):

Drymusidae (Fig. 24), Caponiidae n. subfam. (Fig. 26), Mecysmaucheniidae (Fig. 25), Corinnidae (*Sphingius*) (Fig. 23).

The type of leg surface is one of the most reliable characters in the phylogenetic classification of labidognath spiders, although many recent analyses (Raven 1985; Coddington 1990) have treated this character as only a single character among various main groups of characters.

B. Outgroups

1) The generally accepted outgroup for the whole order Araneae is Amblypygi. The leg skin type of Amblypygi is scaly (PLATNICK & GERTSCH 1976; personal studies), but a review of the other Arachnid orders reveals that this could be an autapomorphy for Amblypygi within the branch Amblypygi + Araneae.

The leg skin structure of the other orders is quite variable (Figs 27-30), with all main types of spider skin also being present in other groups of Arachnida. Frequently, two entirely different types of leg skin are present in the metatarsi and tarsi of a single specimen, as in the opilionids of Stylocellidae (Fig. 30) and Phalangodidae. The scaly leg skin type is common to anactinotrichid mites (Fig. 29) and the ridged type to actinotrichid mites (Fig. 28).

2) There are several alternative outgroups for different suborders of spiders. However, these problems cannot be ultimately resolved by the results of this study.

Liphistiomorpha and Mygalomorpha.

The leg skin structure has been preliminarily studied in various mygalomorph and in both liphistiomorph families. The leg skin structure of Liphistiomorpha (Fig. 31, cf. also PLATNICK & GOLOBOFF 1985) could be classified as scaly, but it is unique among Araneae. Moreover, many of the other ultrastructural characters (structure of the bothrial base and tarsal organ) differ from those of all known labidognath spiders. The heptathelid "scales" are separate, rounded triangular extensions of the skin, well separated by continuous, nearly smooth skin. It is difficult to derive this type from the basic scaly type of Amblypygi, nor do any of the mygalomorph groups seems to share this autapomorphy of the recent Liphistiomorpha.

The leg skin of mygalomorph spiders is much more variable than that of labidognath spiders. The presence of the ridged type has been confirmed in three seemingly unrelated genera (cf. results in p. 3). Various papular surfaces (Fig. 32) as well as nearly smooth surfaces may constitute modifications of the ridged type, but occassionally also of the scaly type (RAVEN & PLATNICK 1981).

Araneomorpha s.lat. (Labidognatha auct.).

Liphistiomorpha and Mygalomorpha together, or Mygalomorpha alone, have usually been suggested as the outgroup for other spiders. However, there are no ultrastructural characters that could directly confirm either of these alternatives. Since PLATNICK's (1977) first phylogenetic analysis of the main spider groups, Hypochilidae, Gradungulidae, and Austrochilidae together have been regarded as the outgroup for other Araneomorpha s.lat. (= Araneoclada).

C. Polarity of evolution

Attempts to use leg skin characters for phylogenetic analysis of the main groups of spiders have failed due to incorrect coding. For example, CODDINGTON (1990: fig. 2 & 3) added character 13/24 to previous matrices (FORSTER *et al.* 1987) as a new hypothesis and coded smooth cuticle plesiomorphic and ridged cuticle as synapomorphy for Gradungulidae, Austrochilidae and Araneoclada. Similarly, RAVEN (1985) coded smooth cuticle as plesiomorphic in some Mygalomorph groups.

Attempts to use bothrial base (CODDINGTON 1990: characters 6,7) have been even more unsuccessful, as the coding is not interpretable and such a "plesiomorphic entire base" claimed for bothria in Araneoclada has never been found by this author outside Araneomorpha s.str. among the hundreds of genera studied.

CODDINGTON (1990: fig 108, ch 49) coded the hair type of all Deinopoidea as "pseudoserrate" and placed this type as an intermediate type between the plesiomorphic plumose and apomorphic serrate (Araneoidea). A study of all possible ultrastructural characters in Uloboridae and many of those in Deinopidae has revealed no differences between the hair structures of Amaurobioidea, Dictynoidea, and Deinopoidea.

The plesiomorphic type of labidognath leg skin is ridged and is also shared by the outgroup Gradungulidae + Austrochilidae. This skin type is present both in the majority of the haplogyne and primitive cribellate groups, as well as in practically all groups of Amaurobiomorpha *sensu* LEHTINEN 1978. The exceptions include some Zodarioidea, Thomisoidea and Nicodamoidea that are here classified as modified branches of Amaurobiomorpha. The surface structure of tarsal claws is ridged in all spider groups studied, although dramatically reduced. The basal part of the tarsal claws often shows some "secondary hairs" (Fig. 33) confirming homology with the normal plumose hairs of Amaurobiomorpha and primitive cribellate group.

The smooth type of leg skin does not deserve much attention here, as it is always an autaopomorphy of a restricted group and is correlated with adaptation to extreme environmental conditions. In most cases with predominantly smooth leg skin, the plesiomorphic pattern of this group can be found from restricted parts of the leg surface, often only in the structure of the bases of normal hairs. Virtually smooth legs have been found in *Atypus* (Atypidae), many haplogyne groups (Sicariidae, Diguetidae, Tetrablemmidae), *Zodarion* (Zodariidae), *Rastellus* (Gnaphosoidea, Ammoxenidae), and *Nesticus* (Araneoidea, Nesticidae, Fig. 17). Published SEM micrographs show that the skin of some other Araneoidean group may be smooth, at least in some details depicted, as in Malkaridae: Sternodinae (PLATNICK & FORSTER 1987) and Cyatholipidae (GRISWOLD 1987). The smooth leg skin of *Brignoliella* (Tetrablemmidae, Tetrablemminae) is divided into parallel, tranverse fields, an autapomorphy that hardly represents a reduction of intervening ridges and furrows.

The density of the furrows varies greatly and reversals between the subtypes seem to be common. The densest furrowing has been recorded from Scytodoidea (Ochyroceratidae and Leptonetidae), while the unmodified furrows of Psechridae are among the most sparse. Frequently, there are thicker ridges separating fields of narrow ridges and furrows, as in *Tangaroa* (Uloboridae; Figs. 1,41-43). The regular ridges and furrows often tend to form more irregular, anastomosing patterns (Figs. 11,12). These autapomorphic patterns, while similar in appearance, certainly have evolved independently in Gnaphosoidea (cf. also PLATNICK 1984 *a*, *b*, 1991), Lycosoidea (PLATNICK & FORSTER 1993) and Corinnidae: Castianeirinae.

Mygalomorpha has not been sufficiently investigated for ultrastructural characters, but the presence of the ridged type in several mygalomorph lineages implies that the ridged type is even plesiomorphic for the whole order.

The polarity of evolution of some repeatedly discussed araneomorph (s.str.) characters must be emphasized here, when attempting a phylogenetic classification of all spider groups. The bothrial pattern of the haplogyne groups (not Caponiidae) and of all Araneomorpha *sensu* LEHTINEN 1978 has earlier been shown to be plesiomorphic (LEHTINEN 1980). The apomorphic patterns of Amaurobiomorpha have occassionally been secondarily reduced in regard to tarsal bothria, though a complete reversal to the plesiomorphic type is not known and can hardly be expected to occur. The plesiomorphic homologue of colulus in Araneomorpha *sensu* LEHTINEN is a long, unpaired, spinneret-like structure, while the corresponding plesiomorphic state of this structure in Amaurobiomorpha is the cribellum. No direct reversals are known for this structure, while the filistatid cribellum could represent homoplasy. The derivation of Araneomorpha s.str. (= Araneoidea auct.) within the RTA-clade in Amaurobiomorpha is impossible, and all further problems can be resolved by acceptance of the parallel evolution of the cheliceral peg teeth (Pholcidae, Palpimanoidea, scattered Araneomorpha s.str.) and the most effective type of web for prey catching, the orb web (Araneomorpha s.str. and Uloboridae).

DISCUSSION

The leg skin structure and related ultrastructural characters of normal and modified leg hairs are a very useful and also practical means for phylogenetic analysis of most suprageneric groups, including at least the main groups of labidognath spiders. The polarity of evolution in leg skin type and most other ultrastructural characters can be easily demonstrated, and the coding of characters is easy, with the exception of some modifications of the bothrial base which still need additional work.

For classification of most spider families, the results of this analysis simply confirm the results of other recent work on spider phylogeny. However, this analysis should provide support for resolving the classification of those groups for which there is strong disagreement. The leg skin structure of Uloboridae, Palpimanidae, Mimetidae, and Nicodamidae needs special discussion here, and for those families many other ultrastructural characters will also need to be summarized.

No reversals from the apomorphic scaly types back to the plesiomorphic ridged type are known and could hardly be expected. The scaly skin type most probably has evolved more than once during the evolution of the order Araneae, as it has certainly done within the class Arachnida. The scaly skin type of the large group Araneomorpha sensu Lehtinen is correlated with numerous character groups outside the ultrastructural characters. This group is therefore easily separated from other spider groups with primarily scaly skin and several, possibly autapomorphic subtypes (Liphistiomorpha, many Mygalomorpha, Zodariidae: Storenidae, Nicodamidae: Nicodaminae). These groups showed entirely different character states, when compared with the other characters of Araneomorpha s.str.

Mygalomorpha. RAVEN (1985) presented the first modern analysis of phylogenetic relationships of Mygalomorph families. Leg skin type was sometimes

included in his matrices (p. 26) as a single character, but unfortunately not in the comparison of all families, and when used, smooth skin was interpreted to be plesiomorphic. Such polarity most probably does not hold for any arachnid group.

The radiation in the evolution of the leg skin types of Microstigmatidae is exceptionally wide (cf. RAVEN & PLATNICK 1981; PLATNICK & FORSTER 1982). *Micromygale diblemma* has unique combination of scaly skin and longitudinal ridges on the bothrial base. These ridges are more widely spaced than in the known ridged patterns in other spider families, and this bothrial type is not considered to represent a reversal of evolution.

The limitation of many mygalomorph families by RAVEN (1985) and GOLOBOFF (1993) is quite different from previous efforts, with both two classifications also differing from each other. The results of the present study support some details of both, but a detailed discussion of the classification of this group is here omitted.

Araneomorpha *sensu* LEHTINEN 1978 (= Araneomorpha s.str.). The limitation of this group must be revised by classifying the Archaeoidea as a primitive sister group of Araneoidea s.lat. (= remaining Araneomorpha s.str.). Deinopidae and Uloboridae were originally excluded as well as all Palpimanoidea s.str. (all with ridged skin). The group diagnosis of Araneoidea s.lat. includes many convincing synapomorphies:

Scaly leg skin; simple bothrial base; only one, serrate type of leg hairs with insignificant modifications; male genital bulbus basically with complex embolic division and apicodorsal modifications of palpal tibia (when present); anterior median spinnerets evolved to an unpaired, elongate colulus, when preserved at all (cribellum never present); subglobular to high oval abdominal shape; and abdominal modifications present in several lines of evolution.

The plesiomorphic state is usually preserved in simple bothrial pattern (no tarsal, one metatarsal); prey caught with non-tubular web; and chelicerae armed with teeth on both margins.

Mimetidae shares all the studied ultrastructural characters with Araneoidea (Figs. 37,39) and its assignment to Palpimanoidea has previously been widely questioned. Finally PLATNICK & SHADAB (1993: 4) admitted that the cheliceral characters "are not ideal" and presented SEM micrographs of the aberrant subfamily Oarcinae, where both the scaly skin and bothrial base are similar to Araneoidea.

Exceptionally smooth skin has also evolved also within this main line of evolution (some Nesticidae), but this observation causes no problems in the phylogenetic assignment of this family.

Archaeoidea & Palpimanoidea. The bothrial base in Mecysmauchenidae and Archaeidae is more complex than in Araneoidea (several concentric ridges in the arched part). Other ultrastructural characters of chitinous parts (also leg skin types) afford transitional states between the ridged and scaly types, with the type of genital organs being more primitive than in any other "Araneoclada". Archaeidae and Mecysmaucheniidae (Fig. 25) were placed on top of the cladogram of Palpimanoidea (FORSTER & PLATNICK 1984), though all their leg skin characters are plesiomorphic,

when compared with Mimetidae and Micropholcommatidae (Figs 37-39). The results above suggest derivation of all Araneoidea s.lat. from Archaeoidea, but even then Uloboridae must be excluded and it cannot be placed together with other orb-weavers.

Palpimanoidea s.str. (= Palpimanidae *sensu* SIMON 1903, including Stenochilidae, and Huttoniidae) are probably primitive relatives of Amaurobiomorpha, although many of their characters are strongly modified due to adaptations. The original ridged type is found even in the most modified Palpimanidae (*Steriphopus* & *Palpimanus*), where some parts of the femur and most of the bases of normal hairs even in the more distal segments have these ridges, although most of the leg surface is smooth or irregularly modified (Fig. 16). A considerably more ridged form of leg skin has been preserved in the more plesiomorphic *Otiothops* (Fig. 8), as well as in Stenochilidae (*Colopea*).

The polyphyly of Palpimanoidea *sensu* FORSTER & PLATNICK 1984 seems to have now been finally confirmed and the presence of cheliceral peg teeth, the main "synapomorphy" for that group, is found to be convergent in spiders. Palpimanidae and Stenochilidae share the Amaurobiomorph type of normal hair structure and the number of hair types. While, the most often studied ultrastructural character, the type of the bothrial base, is aberrant but not comparable with any of the bothrial base types present in the Araneomorpha s.str. with scaly skin.

Amaurobiomorpha *sensu* LEHTINEN 1978/RTA-clade *sensu* CODDINGTON & LEVI 1991. Amaurobioidea, Dictynoidea, Lycosoidea, Clubionoidea, Heteropodoidea, and Pisauroidea all share the plesiomorphic leg skin type and many other plesiomorphic morphological characters. Gnaphosoidea and Salticoidea are generally more apomorphic, but are easily assigned to the main branch of Amaurobiomorpha. Zodarioidea, Corinnoidea, and Thomisoidea each have several autapomorphies but most probably do belong within this group.

Deinopoidea *sensu* CODDINGTON 1990 was originally and is still included in Amaurobiomorpha. Its possible derivation from Psechridae/Titanoecidae has been reviewed by SHEAR (1994). All claimed synapomorphies for Deinopoidea and Araneoidea sensu CODDINGTON, 1990 (p. 33 fig. 3: 11-16; fig. 108: 44-46, 49, 64-65, 67-69, 73, 77-78, 81-82) are characters either wrongly coded (108: 49) or strictly connected to a single adaptation, i.e., the use of orb web or its derivatives, with most of these (3:11-16; 108: 64-82) not being structural but ethological. The type of leg skin (Figs. 1, 41-43), the presence of many different types of leg hairs (including even feathery hairs: Fig. 44), the type of bothrial base and tarsal organ (Figs. 42-43), the sexual dimorphism of leg spinulation, and the presence of cribellum are all typical Amaurobiomorph characters. However, the details of the genital organs of Deinopoidea cannot be homologized with Araneomorph genitalia.

The leg skin structure of Amaurobiomorpha and the primitive outgroups (Hypochilidae, Gradungulidae and Austrochilidae) as well as all true labidognath haplogyne groups (Dysderoidea, Scytodoidea, and Caponiidae) is either ridged or secondarily smooth, while the longitudinally ridged bothrial base is dominant througout these lines of evolution, strongly suggesting the plesiomorphic state of the ridged skin and longitudinally ridged bothrial base in labidognath spiders.

The anterior median spinnerets are represented by a bipartite cribellum that may lose its central septum, when reduced to a "pseudocolulus" (nonfunctional cribellum), this intermediate structure is always flat, not conical or fingerlike as a true colulus.

The most important synapomorphies for Amaurobiomorpha are: abdominal colour pattern with anterocentral folium; complex bothrial pattern (several metatarsal, a tarsal row with increasing length); numerous types of plumose hairs and sensory hairs; web with a basal tube, but often further modified or reduced (hunting habits).

Leg scopulae are never present in Araneomorpha s.str., but this is typically an adaptive character and possibly evolved several times within Amaurobiomorpha.

Distal bulbal as well as vulval and epigynal homologies between different main groups of spiders have been widely discussed and are very hard to prove. The genital structures of Amaurobiomorpha generally have many more similarities to each other than to those of any groups of Araneomorpha, but these characters are excluded here as strong evidence for any phylogenetic relationships. It must be noted here that genera with "palpal conformation" (cf. MILLIDGE 1977) of very different types and tegular processes ranging from none to four complex processes are sometimes found within a single family (Ochyroceratidae).

CODDINGTON & LEVI (1991:581) introduced the group "RTA Clade" which appears to be almost the same as Amaurobiomorpha. However, they excluded all groups that were insufficiently known (Cycloctenidae, Miturgidae, all Zodarioidea, Nicodamidae) as well as the "Lower Entelegynes" (Oecobiidae, Hersiliidae, and Eresidae), Palpimanidae s.lat. and Deinopoidea. RTA-Clade does not include any groups outside the original Amaurobiomorpha and could be called Amaurobiomorpha s.str. or sensu Coddington & Levi. The presence of a retrolateral tibial apophysis in the male palp is useful as such, but it has been reduced within the RTA Clade, at least in most Lycosidae, and shows parallel evolution in several groups of Araneomorpha s.str. Moreover, it is also present within the Eresid genus *Wajane*, as well as in problematic groups, placed by CODDINGTON & LEVI (1991) to "other" entelegynes.

Groups with disputable relationships

1) Thomisidae/Philodromidae. All Thomisidae have strongly modified leg skin (Figs. 13,14), at least partly papular. The leg skin of Philodromidae is ridged and similar to that of Heteropodidae. Feathery hairs are common to all Philodromids studied so far, but absent in Thomisidae, thus supporting the separation of Philodromidae from Thomisidae, originally based on other morphological characters (HOMANN 1975; DONDALE & REDNER 1976).

2) Corinnidae/Trachelidae/Liocraniidae/Phrurolithinae: Numerous genera of these groups have recently been transferred to other families (PENNIMAN 1985, PLATNICK & UBICK 1989, CODDINGTON & LEVI 1991, PLATNICK & DI FRANCO 1992, PLATNICK & BAPTISTA 1995). Several other genera were examined in this study with regard to several ultrastructural characters. Ultrastructural characters are quite useful for the definition of these amaurobiomorph groups, but most details will not be further discussed here.

Corinnidae usually shows a strongly modified type of leg skin with numerous modifications also in other ultrastructural characters (Figs. 20,23). However, the ridged type has been preserved in some details within most genera, *Supunna* being the best example. Phrurolithinae has similar, possibly parallel modifications, and both could be derived from somewhere within Amaurobiomorpha.

Both Liocraniidae and Trachelidae are characterized by the plesiomorphic type of ridged leg skin, with other ultrastructural characters being typical of Lycosoidea (Liocraniidae) or Clubionoidea (Trachelidae).

3) Zodariidae/Cryptothelidae: The leg skin tends to be strongly modified in Zodariinae (Fig. 19). The leg skin type of *Storena*, *Mallinella* and *Asceua*, at least, is scaly, although most probably not strictly homologous with other scaly types within Amaurobiomorpha. This is a convincing synapomorphy for this group of genera, though it is not shared by *Leprolochus* (cf. Jocque 1991). The type of leg skin found in Cryptothelidae supports the placement of this group as a sister group of Zodariidae sensu Jocque 1991.

4) Nicodamidae. The leg skin structure of Nicodamidae is best classified as scaly (Fig. 24). However, other ultrastructural characters, especially the presence of plumose hairs and, in general, the presence of several hair types on the legs, are not present in any Araneoidea. For these reasons, the "scaly" leg skin of this subfamily could be an autapomorphy. However, the suggested relationship of Megadictyninae to Nicodaminae (Forster 1970, Harvey 1995) remains problematic, as the leg skin of *Megadictyna* is smooth (Fig. 18) and the evolution from Megadictynine cribellum to the conical colulus of Nicodaminae would be unique.

Ultrastructural characters in future cladistic analysis

This paper has mainly concentrated on the analysis of one important character of a very large character group and has focused on the consequences of previous misinterpretations of the polarity and variation of leg skin type. A cladistic analysis of all spider families/groups with an addition and correction of coding of ca. 15 other ultrastructural characters for leg morphology, as well as about 50-100 additional ultrastructural characters for mouth parts, carapace, abdomen, etc. will be the next necessary step to balance the matrices for a more comprehensive phylogenetic analysis of spider groups. At least, the easily coded characters should be added to the currently used family matrices with one strongly predominating character group (spinnerets and spinning activities). The other, sometimes very large group of characters, the genital organs, is plagued with problems of homology and therefore also with repeated problems of correct coding. Some other commonly used character groups, e.g., spine patterns and cheliceral armature have also shown repeated problems with correct coding. The classification of spiders today is very far from completion, especially with respect to the main groups of spiders above the family level.

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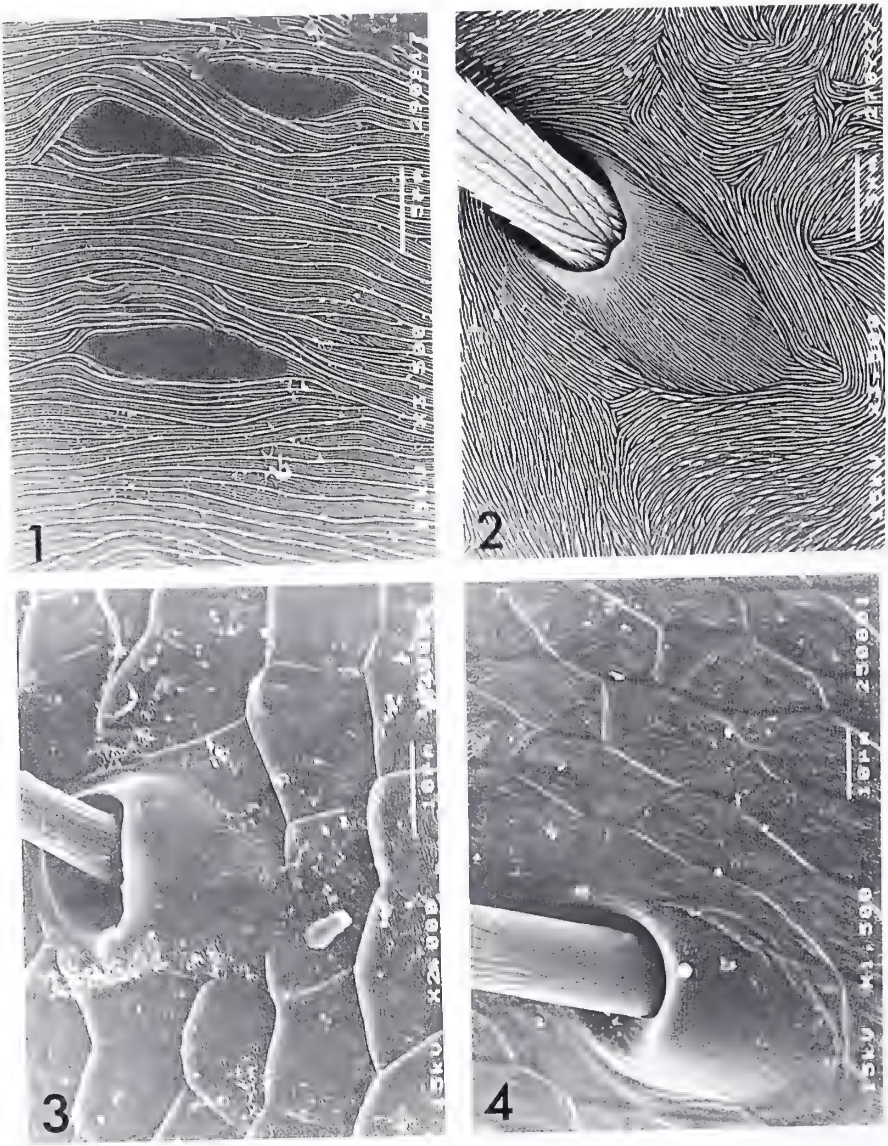
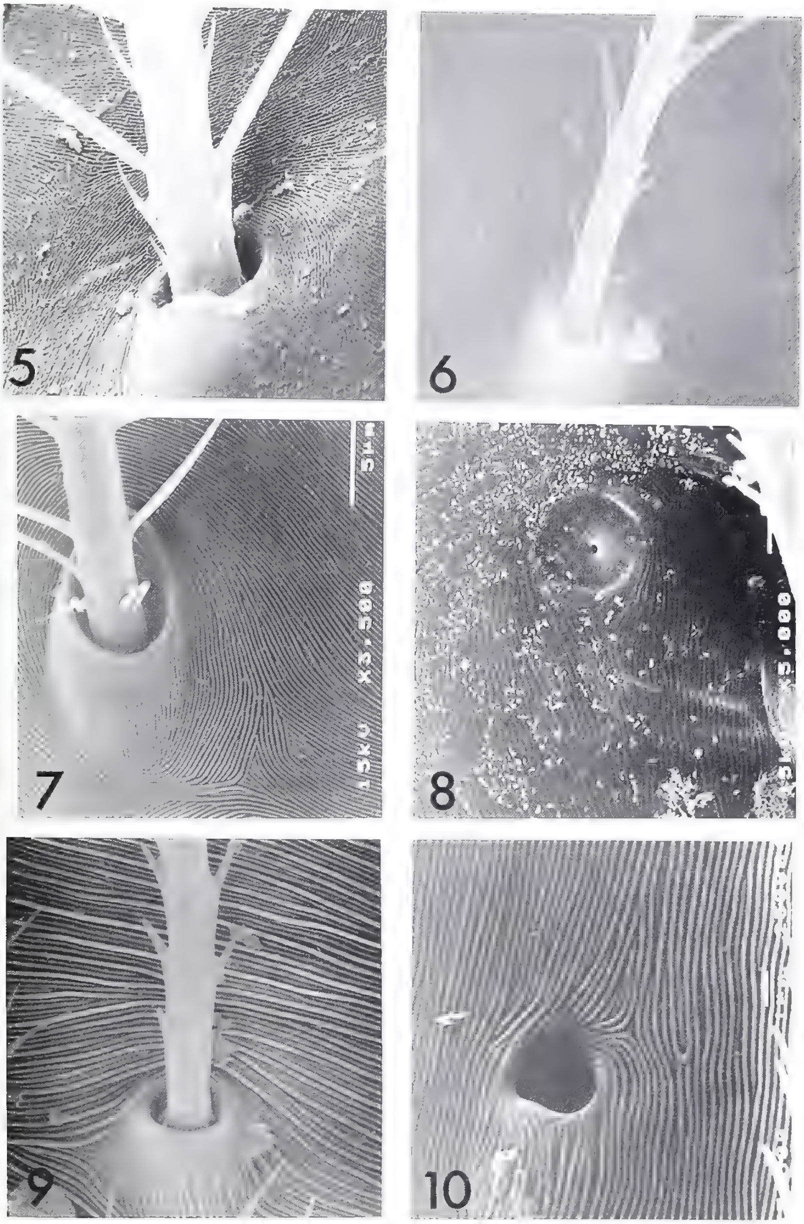
The information about magnification in the SEM-micrographs concerns original magnification in 6 x 9 cm negatives. The exact final magnification can be calculated from the scale bar, when present. The suborder is Araneomorpha s.lat., when not otherwise indicated.



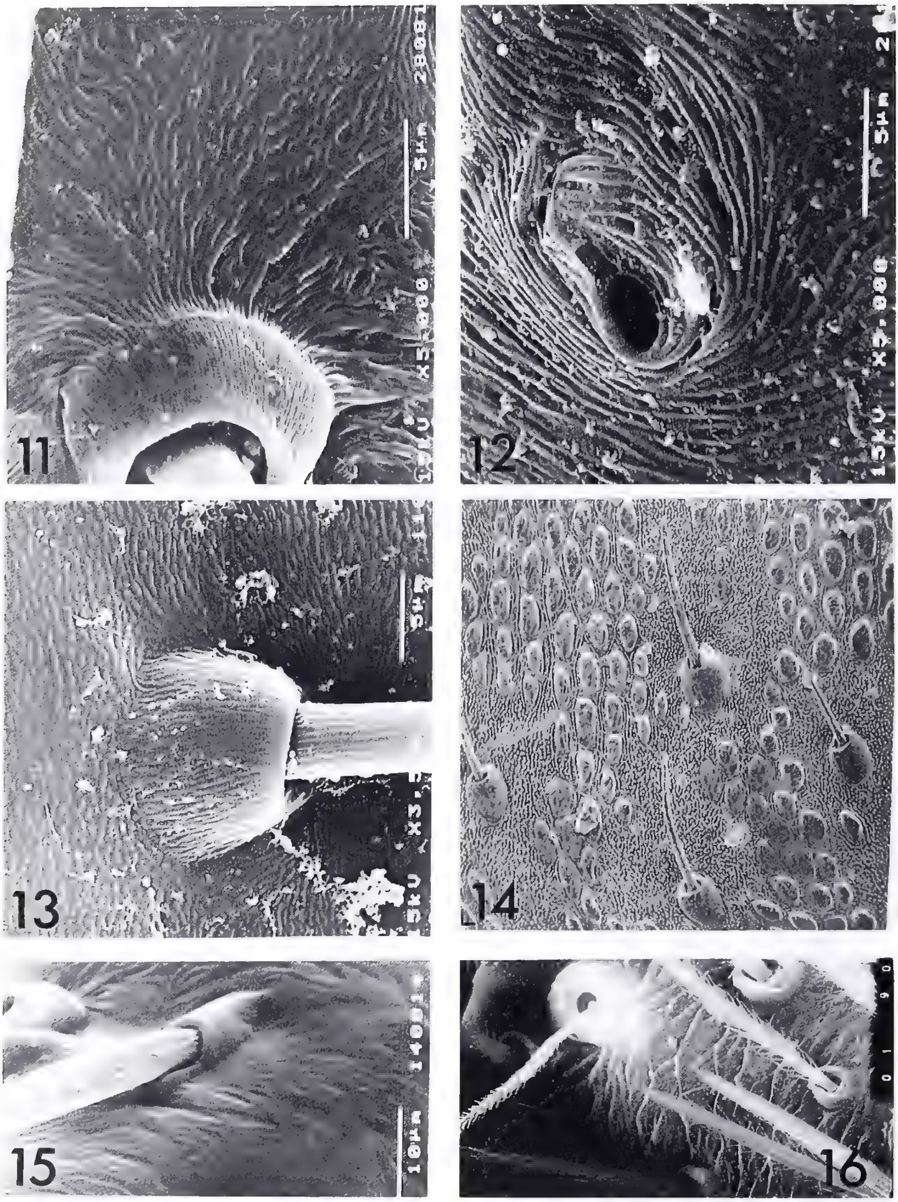
Figs 1-4

Two basic types of leg skin in spiders: 1-2 ridged type, 3-4 scaly type. - 1: *Tangaroa tahitiensis* (Uloboridae), lateral field of palpal tibia; 2: *Psechrus argentatus* (Psechridae), tarsal surface; 3: *Araneus diadematus* (Araneidae), femoral surface; 4: *Hexathele montana* (Mygalomorpha: Hexathelidae), metatarsal surface.



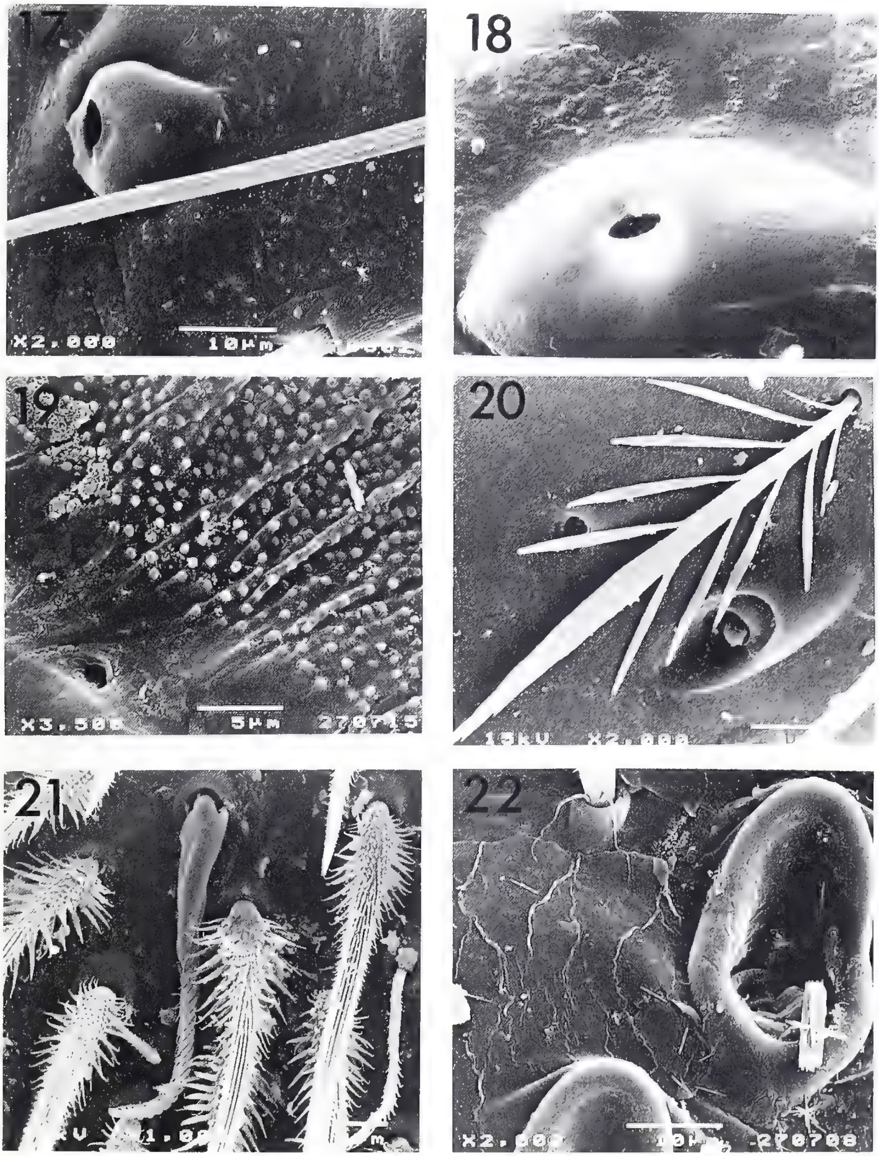
FIGS 5-10

Range of the ridged, plesiomorphic type of leg surface. - 5: *Thaida* sp. from Chile (Thaididae), metatarsal surface; 6: *Encyocrypta* sp. from New Caledonia (Mygalomorpha: Barychelidae), tarsal surface; 7: *Gradungula sorenseni* (Gradungulidae), tarsal surface; 8: *Otiothops* sp. from Peru (Palpimanidae: Otiothopinae), surface of tarsus IV with tarsal organ; 9: *Thasyraea* sp. from Australia (Zoridae), tarsal surface; 10: *Miturga agelenina* (Miturgidae), tarsal surface with sensory pit of unknown function.



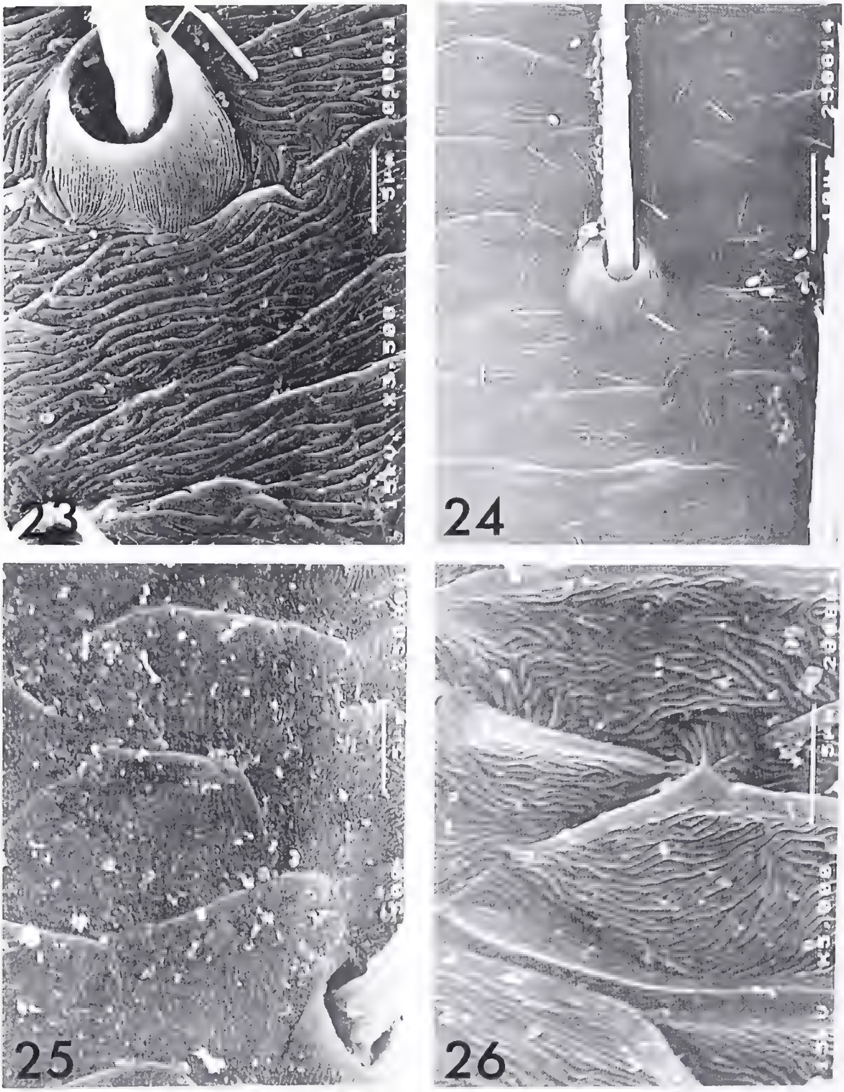
FIGS 11-16

Modified types of leg surface. - 11: *Hersilia pectinata* (Hersiliidae), metatarsal surface with anastomosing ridges; 12: *Rhene* sp. from Flores (Salticidae), tarsal surface with tarsal organ, weakly anastomosing type; 13: *Porropis nitidula* (Thomisidae), metatarsal surface of weakly modified thomisid type; 14: *Xysticus audax* (Thomisidae), papular tibial surface; 15: *Leprolochus* sp. from NE Brazil (Zodariidae), irregularly modified, almost smooth tarsal surface; 16: *Steriphopus* sp. from Indian Himalaya (Palpimanidae), scaly tip of metatarsus close to weakly ridged area.



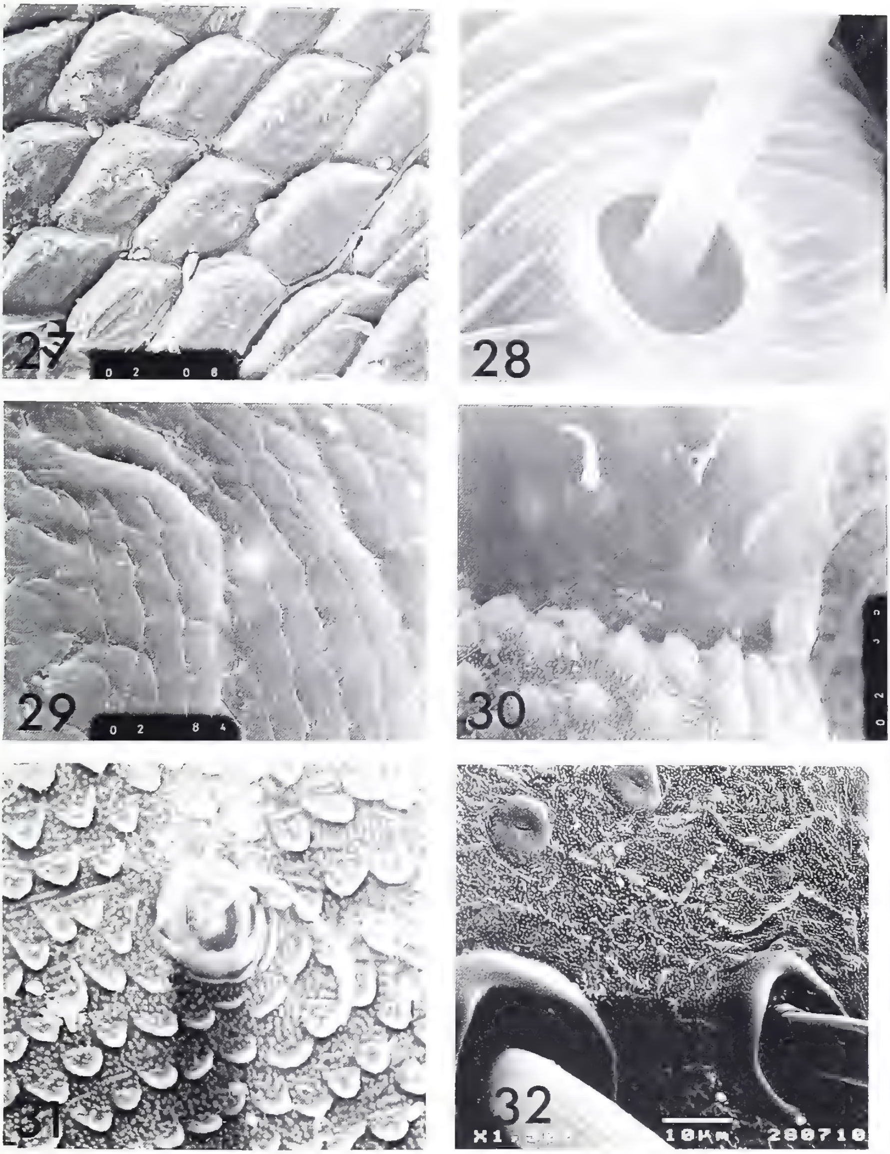
FIGS 17-22

Smooth and modified types of leg surface. - 17. *Nesticella nepalensis* (Nesticidae), smooth tarsal surface; 18: *Kukulcania hibernalis* (Filistatidae), smooth tarsal surface around tarsal organ; 19: *Zodarion trispinosum* (Zodariidae), femoral base, partly with papular surface; 20: *Creugas gulosus* (Corinnidae: Corinninae), smooth metatarsal surface; 21: *Adonea variegata* (Eresidae), smooth metatarsal surface; 22: *Homalonychus theologus* (Homalonychidae), smooth tarsal surface with irregular "scaly" pattern.



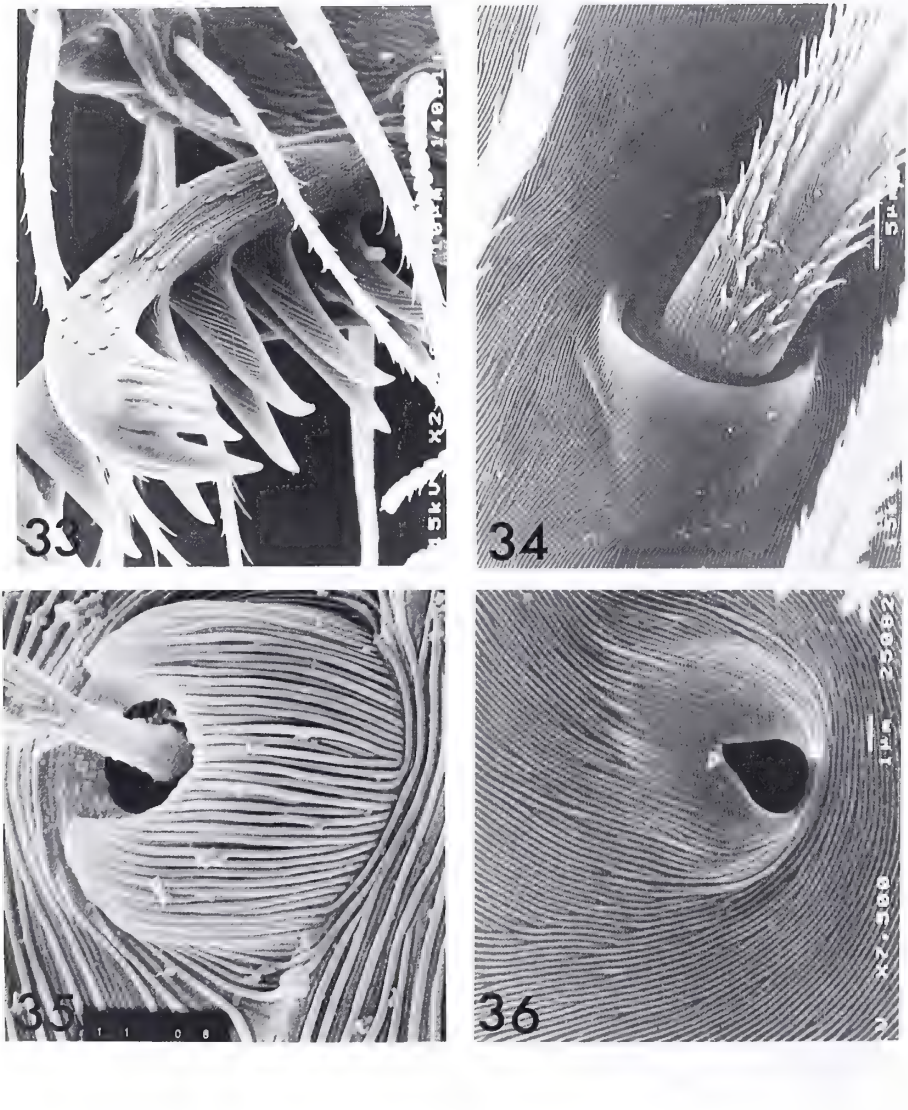
Figs 23-26

Mixed leg surface patterns. - 23: *Sphingius* sp. from Sri Lanka (Corinnidae: ? subfamily), tarsal surface; 24: *Drymusa silvicola* (Drymusidae), metatarsal surface; 25: *Mecysmauchenius* sp. from Chile (Mecysmaucheniidae), tarsal surface; 26: N.gen., n.sp. from Vietnam (Caponiidae, new subfamily), metatarsal surface.



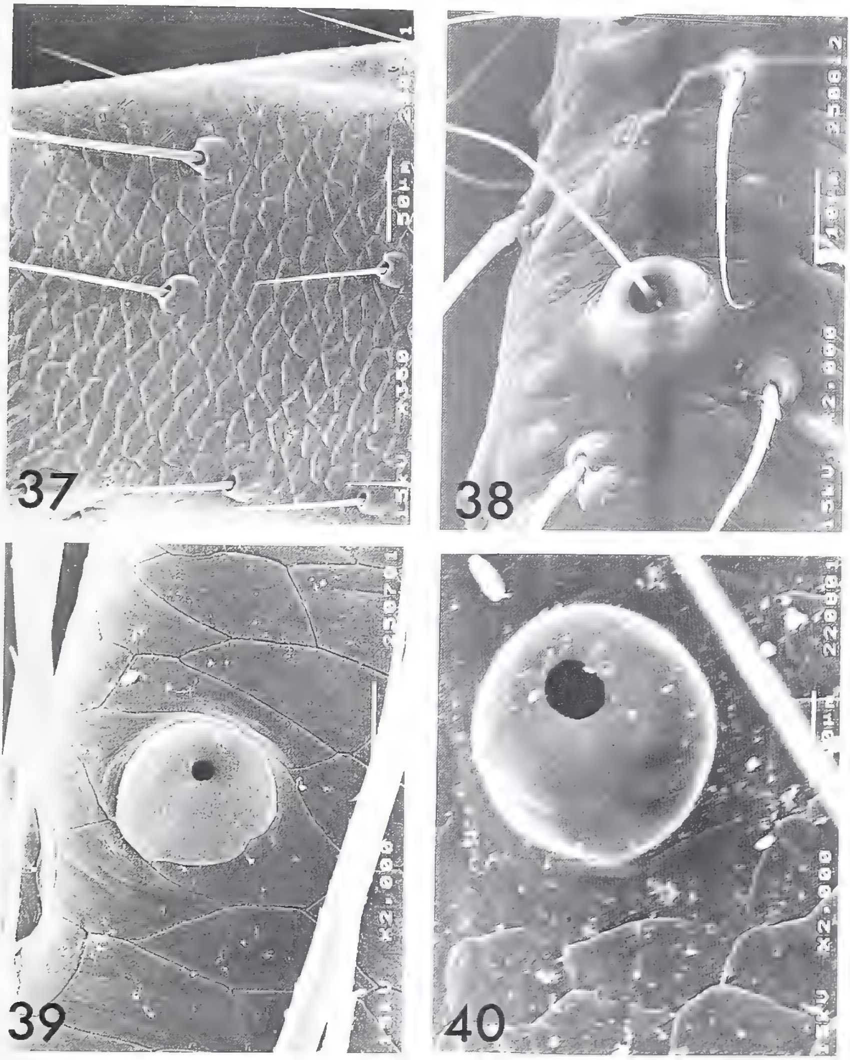
FIGS 27-32

Leg surface in various Arachnid groups. - 27: *Phalangium opilio* (Opilionida: Phalangiidae), scaly tarsal surface; 28: *Trombidium* sp. from Finland (Actinotrichida Parasitengona: Trombidiidae), ridged metatarsal surface; 29: *Ixodes ricinus* (Anactinotrichida Ixodida: Ixodidae), scaly femoral surface; 30: *Stylocellus* sp. from New Caledonia (Opilionida Cyphophthalmi: Stylocellidae), papular metatarsal and scaly tarsal surface; 31: *Liphistius malayanus* (Liphistiomorpha: Liphistiidae), metatarsal surface; 32: *Aname pexa* (Mygalomorpha: Nemesiidae), modified tarsal surface of liphistid type.



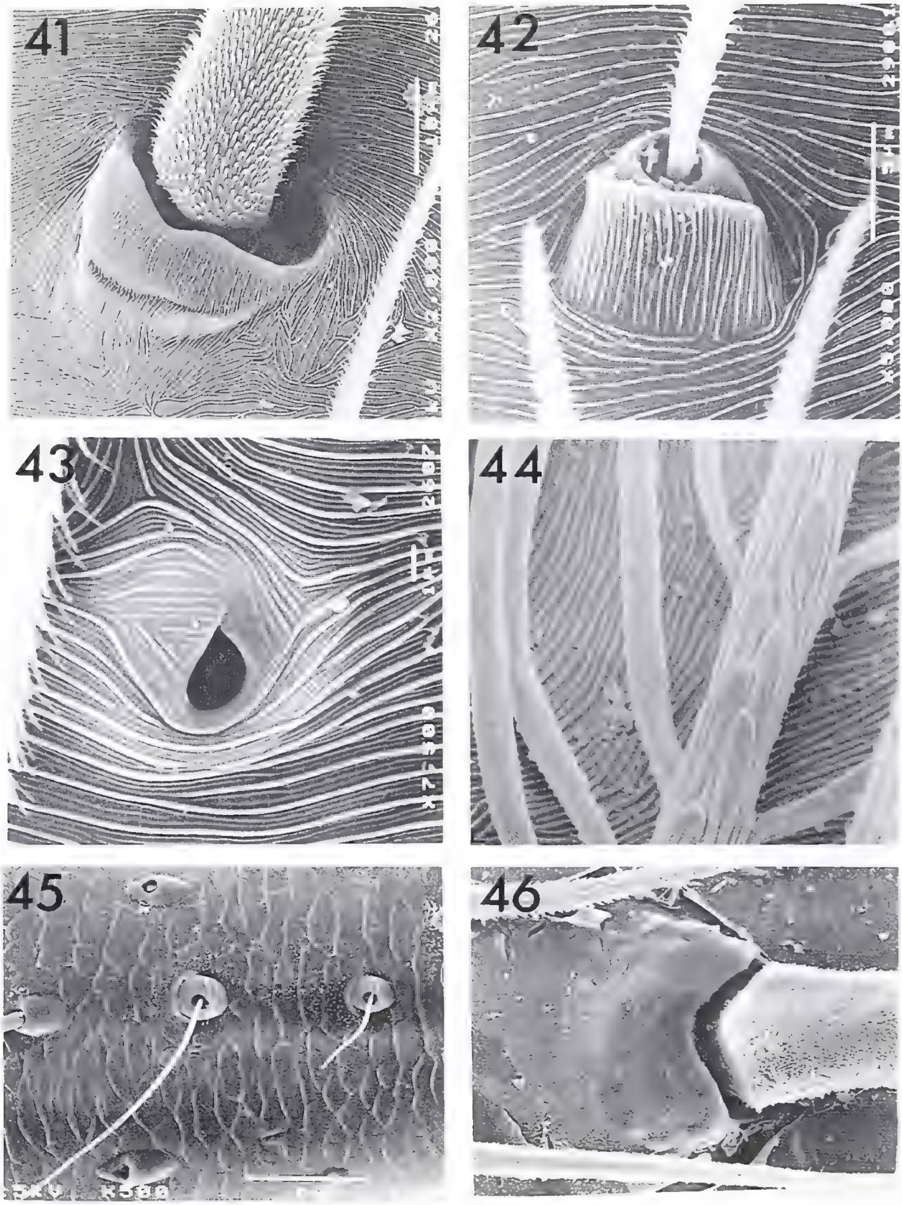
FIGS 33-36

Extension of the plesiomorphic surface pattern to other leg structures. - 33: *Leprolochus* sp. from NE Brazil (Zodariidae), surface of tarsal claws; 34: *Miturga agelenina* (Miturgidae), surface of plumose tarsal hair; 35: *Hahnia pusilla* (Hahniidae), completely ridged metatarsal bothrial base; 36: *Cycloctenus* sp. from New Zealand (Cycloctenidae), completely ridged tarsal organ.



Figs 37-40

Araneoidean type ultrastructure of doubtful "Palpimanoidea" with cheliceral peg teeth. - 37: *Ero furcata* (Mimetidae), femoral surface; 38: *Micropholcomma* sp. from New South Wales (Micropholcommatidae), theridid type of scaly skin with theridid type of tibial bothrial base; 39: *Ero furcata* (Mimetidae), tarsal surface with tarsal organ; 40: *Araneus diadematus* (Araneidae), tarsal surface with tarsal organ for comparison.



FIGS 41-44

Amaurobiomorph ultrastructure of Dinopoidea. Figs. 45-46. Dissimilar ultrastructure of Nicodamidae and Megadictynidae. - 41: *Tangaroa tahitiensis* (Uloboridae), femoral spine with plumose type of secondary hairs; 42: *Tangaroa tahitiensis* (Uloboridae), ridged bothrial base; 43: *Tangaroa tahitiensis* (Uloboridae), non-domed tarsal organ with ridged surface; 44: *Menneus camelus* (Dinopidae), tibial feathery hair with ridged structure extending to the whole stem. - 45: Nicodamidae sp. from Tasmania, scaly tibial surface with non-serrate hairs; 46: *Megadictyna thileniusi* (Megadictynidae), smooth metatarsal surface with plumose type of spine.

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Prey-specific capture behaviour and prey preferences of myrmicophagic and araneophagic jumping spiders (Araneae: Salticidae)

Daiqin LI & Robert R. JACKSON
Department of Zoology, University of Canterbury, Private Bag 4800, Christchurch, New Zealand.

Prey-specific capture behaviour and prey preferences of myrmicophagic and araneophagic jumping spiders (Araneae: Salticidae). - As prey for salticids, ants and spiders both can be dangerous. Not surprisingly, these dangerous prey appear not to dominate the diet of most salticid species. However, an interesting minority of salticid species routinely preys on either ants ('myrmicophagic salticids') or spiders ('araneophagic salticids'). We review recent work on two facets of behavioural specialization in myrmicophagic and araneophagic salticids: prey-specific capture behaviour and prey preferences. We suggest that predators evolving prey-specific capture behaviour against dangerous prey also tend to evolve distinctive preferences for these dangerous prey. Exceptionally acute eyesight, made possible by the unique, complex eyes of salticids, has probably facilitated the evolution of pronounced prey-specific capture behaviour and prey preferences in these spiders.

Key-words: Spiders - salticids - specialization - capture behaviour - prey preference - myrmicophagy - araneophagy

INTRODUCTION

The Salticidae is a large (over 4000 described species) and diverse family of spiders (Coddington & Levi 1991) with unique, complex eyes and acute vision (Land 1969*a*, *b*; Blest *et al.* 1990). The typical prey of salticids tend to be soft-bodied, more or less safe insects such as flies, and acute vision probably enables salticids to avoid contacting potentially dangerous prey. However, in this paper, we consider salticids that specialize on potentially dangerous ants and spiders (Nentwig 1986), prey that are rarely dominant in the diet of most salticid species. However, an

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interesting minority of salticid species routinely preys on either ants (`myrmicophagic salticids') or spiders (`araneophagic salticids') (RICHMAN & JACKSON 1992). In the present paper, we review recent work on two facets of behavioural specialization in myrmicophagic and araneophagic salticids: prey-specific (*i.e.*, specialized) capture behaviour and prey preferences. However, because the term "specialized" has been applied to both a predator's diet and its predatory behaviour, it is important to first specify how the term "specialized" is used here.

Stenophagous versus euryphagous predators

The diets of predators are often described as stenophagous or euryphagous and as specialized or generalized, where the terms "stenophagous" and "euryphagous" refer to the breadth of food resource utilization (*e.g.*, MORSE 1971; FOX & MORROW 1981). Predators are considered to be stenophagous if their diets include only a narrow range of prey types (one or a few) and euryphagous if their diets include a wide range of prey types. It is useful to use "stenophagous *versus* euryphagous" to refer to the predator's diet and "specialized *versus* generalized" to refer to the predator's behaviour (see JACKSON & VAN OLPHEN 1991, 1992).

Predators with prey-specific capture behaviours are behaviourally specialized. A stenophagous predator may or may not have evolved prey-specific ("specialized") capture behaviour for use against the few types of prey in its diet. A euryphagous predator might be "specialized" or "generalized" in capture behaviour. That is, an euryphagous predator may use generalized (unspecialized) capture behaviour against the numerous types of prey on which it normally feeds. Alternatively, a euryphagous predator may be "versatile" (CURIO 1976): it might use a conditional predatory strategy consisting of a repertoire of disparate prey-specific capture behaviours, each adaptively fine-tuned to a different type of prey in its broad diet. A versatile predator is, therefore, euryphagous in diet but behaviourally a specialist on multiple prey types.

An additional distinction is based on preference for prey types. A predator's prey preference is distinct from its actual diet and also from its capture behaviour. Preference, which implies ability to distinguish between different types of prey and choose one rather than another, cannot be inferred simply from knowing the animal's diet in nature or from knowing that the animal has prey-specific capture behaviour.

Specialization in the Salticidae

Spiders as a group are generally envisaged as more or less euryphagous in diet (BRISTOWE 1941; FOELIX 1982; WISE 1993). Yet, scattered reports in the literature (see NENTWIG 1986) suggest that stenophagy, prey-specific capture behaviour and distinctive preferences for unusual prey may be common. The present review is restricted to the Salticidae, a family that has two groups of species with especially pronounced predatory versatility - ant-eating (myrmicophagic) species and spider-eating (araneophagic) species (RICHMAN & JACKSON 1992).

Detailed information about diet, which depends on field studies, is generally absent from the literature on salticids, but all salticids, including the myrmicophagic and araneophagic species, appear to be more or less euryphagous (EDWARDS *et al.* 1974; JACKSON 1977; CUTLER 1980). The present review, therefore, will concentrate on recent laboratory studies of prey-specific capture behaviour and prey preferences.

PREY-SPECIFIC CAPTURE BEHAVIOUR

FORSTER (1977, 1982) analyzed in detail the visually-mediated hunting sequences prevalent in salticid species. The salticid first orients by swivelling its cephalothorax around to bring the principal (AM) eyes to bear on the prey. Next, it aligns its abdomen with its cephalothorax and begins a pursuit, usually by stalking slowly in an almost cat-like manner, towards the prey. When close, the salticid lowers its body and fastens a dragline to the substrate, pauses, then leaps onto the prey. Although this appears to be the typical predatory sequence for most salticid species, myrmicophagic and araneophagic salticids are exceptions.

Araneophagic salticids

Eating other spiders appears to be an opportunistic occurrence for most spiders, a larger or faster individual overpowering another in a chance encounter, but there are numerous exceptions. Some salticids make a practice of leaping or walking into webs to catch the resident spider (TOLBERT 1975; ROBINSON & VALERIO 1977; JACKSON 1985*a*, *b*, 1986, 1988). However, the most extreme specialization on spiders as prey known is in ten species of salticids (from 4 genera), all from the subfamily Spartaeinae (WANLESS 1984). These species practise vibratory aggressive mimicry in other spiders' webs, where they sometimes capture spiders larger than themselves. In the present review, the term `araneophagic salticids' is restricted to these species (JACKSON 1992*a*). Each of these species also preys on insects (either in or out of webs), and the Queensland *Portia fimbriata* also preys on other salticids. A large spider (because it is dangerous), another salticid (because it can see well) or a spider in a web (because it is in a special environment - a web) would all seem to be something that a salticid, as a predator, would perceive as special. The most important common factor is probably that these spiders tend to be, for salticids, difficult-to-catch and dangerous potential prey - the potential prey is also a potential predator.

In a web, an araneophagic salticid's strategy is usually not simply to stalk or chase down the resident spider but instead to send vibratory signals across the silk (aggressive mimicry). The resident spider may respond to these signals in a way that appears indistinguishable from how it would respond to a small insect ensnared in the web, but when the duped spider gets close, the araneophagic salticid lunges out and catches it.

The most extensively studied araneophagic salticids are from the genus *Portia*, and in these species aggressive mimicry is combined with pronounced behavioral

complexity (JACKSON & POLLARD 1996). *Portia* has a large repertoire of vibratory signals (JACKSON & WILCOX 1993*a*) made by manipulating, plucking and slapping the silk with one or any combination of its legs and palps, all of which can be moved in different ways. *Portia* also makes signals by flicking its abdomen, and abdominal movements can be combined with all of the appendage movements. Many of these behaviours by which *Portia* makes signals appear to be evolutionary modifications of grooming behaviour (JACKSON & HALLAS 1990).

The web-building spider, *Portia*'s intended victim, has acute abilities to detect and discriminate between vibratory signals transmitted over the silk in its web, but how the spider interprets these web-borne vibrations varies considerably between species and also with the sex, age, previous experience and feeding state of the spider (WITT 1975; JACKSON 1986; MASTERS *et al.* 1986). Yet *Portia* has been observed using aggressive mimicry to catch many kinds of web-building spiders, within a range of about one tenth to twice *Portia*'s size (JACKSON & BLEST 1982*b*; JACKSON & HALLAS 1986a). Preliminary results suggest that the key to *Portia*'s success at victimizing so many different types of spiders is an interplay of two basic ploys: 1) using prey-specific (fixed) signals when cues from some of its more common prey species are detected (JACKSON & WILCOX 1990); and 2) using feedback to adjust signals to different prey species (JACKSON & WILCOX 1993*a*). The first ploy, using fixed tactics, is consistent with the popular potrayal of spiders as animals governed by instinct. With the second ploy, *Portia* solves problems: *Portia* determines, by trial and error, what to do with different victims. Other problem-solving abilities include making detours when approaching prey (JACKSON & WILCOX 1993*b*; TARSITANO & JACKSON 1993, 1994) and smokescreen behaviour (WILCOX *et al.* 1996).

A number of spider species from several families other than the Salticidae are also web-invading araneophagic spiders that use aggressive mimicry (JARMAN & JACKSON 1986; JACKSON & WHITEHOUSE 1986; WHITEHOUSE 1986; JACKSON & BRASSINGTON 1987). However, web-invading araneophagic salticids appear to differ in important ways from the web-invading araneophagic spiders of other families. Araneophagic salticids can walk across both ecribellate and cribellate sticky webs without getting stuck (JACKSON 1986), and they are highly effective at preying on a wide array of web-building spiders. In contrast, none of the araneophagic non-salticid spiders studied can cross both cribellate and ecribellate sticky webs unimpaired. Also, the set of web-building spiders caught by araneophagic non-salticid spiders is considerably smaller than that of the araneophagic salticids, and the predatory strategies of the araneophagic non-salticid spiders appear to be less complex than those of the araneophagic salticids (JACKSON 1992*a*). Signal output variation appears important in enabling both salticid and non-salticid aggressive mimics to achieve fine control over the responses of each particular victim spider. However, compared to the araneophagic non-salticid spiders, the araneophagic salticids use a larger repertoire of vibratory signals and they combine and vary their signals more extensively. Unlike the araneophagic non-salticid spiders, the araneophagic salticids have acute vision (JACKSON & BLEST 1982*a*) and are not restricted to interpreting web vibrations when detecting, identifying, and locating prey on webs. The absence of acute vision may

have been an important constraint limiting the range of prey taken by the araneophagic non-salticid spiders (JACKSON 1986, 1992*a*).

Although not so extensively studied as *Portia*, the other aggressive-mimic salticids (*Brettus*, *Cyrba* and *Gelotia*) also readily invade many different types of webs and also resemble *Portia* by using strategies based on a combination of fixed signals and trial-and-error behaviour (JACKSON & HALLAS 1986*c*; JACKSON 1990*a*, *b*). However, the genera of araneophagic salticids differ markedly in the methods used for catching prey. For example, *Brettus*, *Cyrba* and *Gelotia* are generally more inclined than *Portia* to remain near the edge of the web (JACKSON & HALLAS 1986*c*). However, the most well-studied differences are among the species, and even populations of single species of *Portia*.

The most pronounced example of interpopulation difference in predatory behaviour is the Queensland population of *P. fimbriata*, which differs from all other *Portia* studied by having special methods for catching cursorial salticids belonging to other genera. *P. fimbriata*'s habitat in Queensland is unique among those studied in having an abundance of cursorial salticids (JACKSON & HALLAS 1986*a*) and, apparently, the Queensland *P. fimbriata*'s predatory behaviour is specially adapted to this locally abundant type of prey (JACKSON 1992*b*).

In the open, the Queensland *P. fimbriata* uses cryptic stalking, a special kind of trickery, but not an example of aggressive mimicry (JACKSON & BLEST 1982*b*). The Queensland *P. fimbriata*, in common with all *Portia*, has an unusual (cryptic) appearance; because of markings, tufts of hairs, and long, spindly legs, *Portia* resembles a piece of detritus and a slow, choppy gait probably helps a moving *Portia* preserve detritus resemblance. Crypsis, which probably provides *Portia* with protection against its own visually hunting predators, is also important in relation to cryptic stalking. When cryptically stalking a salticid, *P. fimbriata* moves especially slowly, pulls its palps back and out of its prey's view, and freezes if the salticid turns to face it, thereby concealing itself from this special type of prey spider which, in common with *Portia*, has acute eyesight. Eventually, the Queensland *P. fimbriata* approaches the salticid from behind, then swoops down to kill it. In addition, the Queensland *P. fimbriata* is unique among *Portia* studied because it makes vibratory signals on the nests of salticids to entice them out and catch them (JACKSON & HALLAS 1986*a*). Furthermore, the Queensland *P. fimbriata* has a special tactic for catching *Euryattus*, a salticid sympatric with the Queensland *P. fimbriata*, but not sympatric with any other *Portia* studied: the Queensland *P. fimbriata* mimics the unique courtship signals of *Euryattus* males to lure *Euryattus* females out of suspended rolled-up leaves and attack them (JACKSON & WILCOX 1990).

Myrmicophagic salticids

Ants come equipped with strong mandibles, poisonous stings and formic acid (EISNER 1970; BLUM 1981). Also, being social insects, ants tend to be present in large numbers and can mount communal attacks on predators and prey (WILSON 1971; HOLLDOBLER & WILSON 1990). All of these factors tend to present formidable

challenges to most cursorial spiders (NENTWIG 1986). However, in most terrestrial environments, and especially in the tropics (where salticids appear to be the dominant spider family: (BRISTOWE 1941), ants are the dominant arthropods in the size range of the prey normally taken by salticids (HOLLDOBLER & WILSON 1990). For a salticid that overcomes the ant's defence, a rich food resource becomes available.

Ants and certain other arthropod groups (*e.g.*, bees, wasps, carnivorous bush-crickets, etc.) present salticids with a problem similar to spiders as prey: they are unusually difficult-to-catch and dangerous, and apparently one of the most effective ways for salticids to exploit ants is with specialized (*i.e.*, prey-specific) capture behaviour. Also, for ants, as for spiders, apparently only a minority of salticid species routinely preys on these heavily defended prey (see ROBINSON & VALERIO 1977). The capture behaviour of 9 myrmicophagic salticid species (6 belonging to subfamily Heliophaninae and 3 to subfamily Euophrynae) has been studied in detail and each of these 9 species preys not only on ants but also on other (more conventional) prey insects (*e.g.*, flies). Each has evolved prey-specific capture behaviour for use against ants, which differs from the predatory behaviour they use to capture other insects (EDWARDS *et al.* 1974; CUTLER 1980; WING 1983; JACKSON & VAN OLPHEN 1991, 1992; JACKSON & POLLARD 1996; LI *et al.* in press).

Predatory behaviour used against ants varies among the species, but the six heliophanines are remarkably similar to each other, while differing from each of the three euophryines. Among the euophryines, *Zendorus* (formerly *Pystira*) *orbiculata* differs considerably in behaviour from another two euophryines, *Corythalia canosa* (JACKSON & VAN OLPHEN 1991) and *Habrocestum pulex* (LI *et al.*, in press). *C. canosa* and *H. pulex* resemble each other by manoeuvring to attack the ant head on. However, unlike *C. canosa*, *H. pulex* never holds its body raised while pursuing, attacking and starting to feed on ants. *Z. orbiculata* attacks ants from just about any orientation. However, *Z. orbiculata*, unlike the other myrmicophagic salticids, also often positions itself facing down on ant-infested tree trunks and ambushes ants by lunging down on them instead of actively pursuing them. *H. pulex* resembles the heliophanines by often stabbing ants then backing away. However, *H. pulex* usually attacks ants head-on. The heliophanines (JACKSON & VAN OLPHEN 1992) sometimes attack ants head on, but they also often attack from directly behind the ant. Not only do all these species stab the ant and attack from directly behind it, but they also usually hold legs I elevated while pursuing, attacking and starting to feed on ants. In contrast, *C. canosa* (JACKSON & VAN OLPHEN 1991) tends to hold its cephalothorax, but not its legs I, elevated.

PREY PREFERENCES OF SPECIALIZED SALTICIDS

We ask three questions about araneophagic and myrmicophagic salticids: 1) Do the species with prey-specific capture behaviour for catching dangerous prey (*i.e.*, ants and spiders) prefer these dangerous prey? 2) Do these species prefer certain sizes of prey? 3) Do males and females of these species prefer the same prey?

Testing methods

NENTWIG (1986) investigated the prey preferences of a wide variety of spiders using different types of prey presented sequentially, and he found evidence of selectivity. A similar method used in an early study of *Portia*'s prey preferences (JACKSON & HALLAS 1986*a*) found that *Portia* preferred spiders to insects as prey. Also, there have been three prey-preference studies of *Phidippus audax*, a common North American salticid: each found evidence of selective predation when different prey were presented simultaneously (GIVENS 1978; FREED 1984; ROACH 1987).

However, the studies we now review differ from the above studies of prey preferences: for each species reviewed here, three distinct types of tests for prey preference were carried out (JACKSON & VAN OLPHEN 1991) - 1) one individual of one type of prey presented to a predator at a time on alternate days, sequence decided randomly; 2) two types of prey presented to a predator simultaneously, one individual prey of each type; and 3) feeding predator presented with one individual of an alternative prey type, sequence for alternate days decided randomly. A strength of these testing routines is that, for each salticid species tested, findings from the different test designs can be compared for consistency. Consistent evidence of the same preference across test designs makes conclusions especially convincing.

Taxonomic categories of prey preferred

Each of 9 species of myrmicophagic salticids studied not only uses a prey-specific behaviour for catching ants, and a different prey-specific behaviour for catching other insects, but also has a distinct preference for ants over other varied types of prey as demonstrated by consistent results across Type 1 - 3 tests (JACKSON & OLPHEN 1991, 1992; LI *et al.* in press).

All of the araneophagic salticids that are known to have prey-specific behaviour for catching spiders (*i.e.*, *Brettus*, *Cyrba*, *Gelotia* & *Portia*) also appear to prefer spiders to insects as prey (JACKSON 1992*a*). However, information from detailed studies based on Type 1 - 3 tests is available only for *Portia fimbriata* from Queensland (LI & JACKSON, in press) and *Portia labiata* from Sri Lanka (Li & Jackson, unpubl. data). These studies show that *P. fimbriata* and *P. labiata* are behaviourally specialized as predators on web-building spiders in two distinct ways: besides using prey-specific capture behaviour against web-building spiders (JACKSON 1992*a*), consistent results from Type 1 - 3 tests show that they also have pronounced preferences for web-building spiders to insects (LI & JACKSON, in press).

Queensland *P. fimbriata* are of special interest because of the unusual component of this *Portia*'s diet: they frequently eat other species of salticids in nature (JACKSON & BLEST 1982*b*). Remarkably, not only does the Queensland *P. fimbriata* use specialized prey-catching behaviour against the salticids on which it preys, but also, from consistent results across Type 1 - 3 tests show that they prefer salticids to other spiders as prey (LI & JACKSON, in press). The Queensland *P. fimbriata* appears to have a hierarchy of prey preferences: on a broader scale, it prefers spiders (both cursorial

salticids and web-building spiders) over insects; on a finer scale, it prefers cursorial salticids over web-building spiders.

Portia labiata and the Queensland *P. fimbriata* are behaviourally different because there is no evidence that *P. labiata* uses cryptic stalking or any other prey-specific capture behaviour against cursorial salticids and, in contrast to the Queensland *P. fimbriata*, *P. labiata* is decidedly ineffective at catching cursorial salticids (JACKSON & HALLAS 1986*a*, *b*). The contrast between *P. labiata* and Queensland *P. fimbriata* extends also to prey preferences: results from Type 1 - 3 tests showed that *P. labiata* prefers web-building spiders to cursorial salticids (Li & Jackson, unpubl. data). Evidently, local abundance of cursorial salticids has also shaped the evolution of, not only salticid-specific capture behaviour, but also prey preferences.

The biology of the myrmicophagic and araneophagic salticids studied suggests that, when predators evolve prey-specific capture behaviour for use against dangerous prey, they also tend to evolve distinct preferences for these dangerous prey. Why this might be so is not obvious. Detailed comparative studies of non-salticid predators are needed to clarify how broadly applicable this trend is in animals.

Males and females compared

In nature, males of all species of *Portia* studied resemble females by frequently feeding on web-building spiders (JACKSON & BLEST 1982*b*; Jackson, unpubl. data). Also, males of all species of *Portia* studied use the same prey-specific prey-catching behaviours against web-building spiders as females (JACKSON & BLEST 1982*b*; JACKSON & HALLAS 1986*a*). In the laboratory, an additional similarity has been illustrated: in Type 1 - 3 tests, both the males and the females of the Queensland *P. fimbriata* (LI & JACKSON, in press) and the Sri Lanka *P. labiata* took web-building spiders in preference to insects as prey (Li & Jackson, unpubl. data).

Furthermore, males of the Queensland *P. fimbriata*, in common with females, frequently prey on cursorial salticids (JACKSON & BLEST 1982*b*; Jackson, unpubl. data) and both males and females also use cryptic stalking against cursorial salticids (JACKSON & HALLAS 1986*a*). Also, in Type 1 - 3 tests, both males and females of the Queensland *P. fimbriata* take cursorial salticids in preference to web-building spiders as prey (LI & JACKSON, in press). In contrast, in Type 1 - 3 tests, both males and females of the Sri Lanka *P. labiata* take web-building spiders in preference to cursorial salticids as prey (Li & Jackson, unpubl. data).

Females of spiders appear to have evolved a lifestyle that emphasizes the consumption of large quantities of food as an adaptation for adding yolk to eggs. Males, in contrast, appear to have evolved a lifestyle emphasizing courtship, mating, and searching for females (see VOLLRATH & PARKER 1992). Because male lifespan is generally short and food requirements are smaller than for females, a preference by males for prey smaller than that preferred by females might be expected. Evidence of this difference was first demonstrated for *Phidippus audax*, a common North American and predominantly insectivorous salticid: *P. audax* males tend to take smaller

prey than females (GIVENS 1978). A similar interspecific difference was found in the Queensland *P. fimbriata*: in Type 1 - 3 tests, males Queensland *P. fimbriata* took smaller spiders (both web-building spiders and cursorial salticids) than did females (LI & JACKSON, in press).

Effect of hunger on prey-preference behaviour

Although hunger has numerous influences on the behaviour of predators (CURIO 1976), including salticids (DREES 1952; GARDNER 1964), little is known about how hunger affects the prey-preference behaviour of salticids. Recently, hunger was investigated in araneophagic and myrmicophagic salticids and found to vary among the species studied. In *Corythalia canosa*, *Chrysilla lauta*, *Natta* spp. and *Siler semiglaucus* (JACKSON & VAN OLPHEN 1991, 1992), well-fed individuals had distinct preferences for ants, but these preferences broke down when these myrmicophagic salticids had been starved for two weeks before testing. When starved, these ant-eating species took ants and other insects indiscriminately. However, prey preferences of myrmicophagic *Habrocestum pulex* (LI *et al.*, in press), and araneophagic *P. fimbriata* (LI & JACKSON, in press) and *P. labiata* (Li & Jackson, unpubl. data), were not affected by a 2-week period without food. Why hunger influences these species differently is currently unclear.

THE ROLE OF VISION IN PREY-PREFERENCE BEHAVIOUR

The distinguishing characteristic of salticid spiders is their complex eyes (LAND 1974; FORSTER 1982; BLEST & CARTER 1987; BLEST *et al.* 1990). The principal eyes are responsible for acute vision (HOMANN 1928; LAND 1969*a*, *b*, 1971), allowing the salticid to identify mates, rivals and predators from distances of 30 body lengths or more (JACKSON & BLEST 1982*a*; Jackson, unpubl. data). Exceptionally good eyesight has probably facilitated the evolution of pronounced preference behaviour in these spiders: evidently, these salticids can discriminate, prior to contact, between different types of prey (JACKSON & BLEST 1982*a*).

The cues used by typical salticids for distinguishing between insect prey and other objects such as mates, rivals, enemies and irrelevant stimuli, have been investigated extensively. Shape, symmetry, presence of legs and wings, size, and style of motion (short, jerky movements) are some of the more important features by which these salticids appear to recognize their prey (HEIL 1936; CRANE 1949, DREES 1952; FORSTER 1979, 1982; EDWARDS 1980). However, for salticids with predatory versatility and pronounced prey preferences, we have little information about the cues that influence the various components of the complex predatory strategies. Most of what we know concerns the cues that govern *Portia*'s decisions of whether to enter a web, whether to make signals once in a web, and whether to persist at signalling once started. Seeing a web elicits web entry, but volatile chemical cues from webs of prey spiders do not appear to be important. Seeing a spider in a web increases *Portia*'s

inclination to enter the web. After web entry, cues from the web are sufficient to elicit signalling behaviour, even in the absence of other cues coming directly from the prey spider. Seeing a prey spider or detecting vibrations on the web make *Portia* more prone to signal, but volatile chemical cues from the prey spiders themselves do not appear to be important. Once *Portia* is on a web and signalling, seeing a moving spider and detecting vibrations on the web encourage *Portia* to persist in signalling (JACKSON 1995).

Prey movement is an especially effective stimulus for eliciting orientation and pursuit by typical salticids (DREES 1952; DILL 1975). Different patterns of movement may also permit salticids to distinguish between different types of prey (FREED 1984). However, movement is not always necessary. Anecdotal evidence suggests that typical insectivorous species of salticids occasionally stalk and attack motionless prey (see FORSTER 1985), and *Portia* preys readily on quiescent web-building spiders in nature and in the laboratory (JACKSON & HALLAS 1986*a*). Additionally, in the laboratory *Portia* can distinguish between quiescent spiders, insects and eggsacs using visual cues alone (JACKSON 1995). Also, eleven salticid species, including *Corythalia canosa* (a myrmicophagic salticid) and four species of *Portia* (araneophagic salticids), stalk and attack completely motionless (dead) prey. The myrmicophagic and araneophagic salticids used the same prey-specific capture behaviour with the different kinds of motionless prey that they normally used with the same kinds of living prey (JACKSON & TARSITANO 1993). Also, the prey preferences of two species of araneophagic salticids, the Queensland *P. fimbriata* (LI & JACKSON, in press) and *P. labiata* (Li & Jackson, unpubl. data), and one species of myrmicophagic salticid, *Habrocestum pulex* (LI *et al.*, in press), have been investigated in tests using dead, motionless prey and shown to be the same as in tests using living prey. These studies suggest that cues from prey shape alone are sufficient to elicit prey-specific capture behaviour and prey preferences in salticids.

DREES (1952), in an experimental study using *Evarcha plancardi*, used lures to investigate the cues by which this insectivorous salticid distinguishes between prey (insects, to be attacked) and other salticids (mates or rivals, to be displayed at). He found that an effective model for evoking conspecific displays had to have a central "body" and a series of `legs' on each side, with the legs making appreciable angles. More legs made lures more effective at eliciting displays. In contrast, lures taking a wide variety of forms were effective at eliciting attacks as long as they moved and were not appreciably larger than the salticid. DREES' (1952) experiments suggest that the insectivorous salticid's rule is: "if it moves, find out whether it has legs in the right places; if it does, display; if it does not, try to catch it". However, for myrmicophagic and, especially, araneophagic salticids, the rules must be considerably more complex. The Queensland *P. fimbriata* is perhaps the most complex, as it preys not only on other spiders but also on other species of salticids. The cues by which myrmicophagic and araneophagic salticids distinguish between different types of prey are currently being investigated.

Questions about the cues used by salticids with predatory versatility highlight how far we remain from fully understanding the functioning of the salticid visual

system. Although salticid eyes are large and complex for a spider, this is no primate (LAND 1974). The principal eye lens is only a few millimetres in diameter, and there are only a limited number of receptors in the salticid eye and neurons in the salticid brain. How so small a visual system, with so few components, is able to perform these perceptual feats is currently a mystery.

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The biogeography of scorpions

Wilson R. LOURENÇO
Laboratoire de Zoologie (Arthropodes), M.N.H.N., 61 rue de Buffon,
F-75005 Paris, France.

The biogeography of scorpions. - The biogeographic patterns observed among modern scorpions are the consequence of three major events which can be integrated in the scheme of scales proposed by Udvardy. The distribution of the principal modern groups (i.e. families and genera) is derived from elements (protofamilies and protogenera of Pulmonate-Neoscorpionina) which originated in Laurasia and Gondwanaland during Pangean times. I suggest the following. I. The main factor in the phylogenetic/palaeobiogeographic scale of Udvardy was probably not latitudinal and longitudinal overland migration (dispersion) of elements, which follow the predominantly southward shift of the warm tropical belt. Instead, I visualise a rather more passive vicariant process in association with dispersal in Haffer's (1981) sense, in response to the progressive fragmentation of Pangea. This was followed by continental drift which led to the present configuration of the continents and climates. This suggestion is in accordance with the very poor vagility observed in modern scorpions. II. On the millenial scale, the Pleistocene (post-Pleistoene) biogeography of Udvardy is responsible for the regional level of the biogeographic pattern which, during its settlement, has led to the selection of new lineages and to the extinction of others. III. On the secular scale, the ecological biogeography of Udvardy is a consequence of recent natural or anthropic events. This scale has been little used by scorpion biogeographers, mostly because of lack of data on scorpion life history strategies. In this contribution, examples from scorpions are proposed for and discussed in relation to the three biogeographic scales of Udvardy.

Key-words: scorpion – biogeography – phylogeny – palaeobiogeography – Pangea – Laurasia – Gondwanaland – Pleistocene – ecology.

INTRODUCTION

Attempts to use scorpions as global model organisms in biogeographic studies are not recent. Starting with the classical contributions of, POCOCK (1894), KRAEPELIN (1905) and BIRULA (1917), general biogeographical traits or patterns began to

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established for this taxon of animals, even though the viewpoints of the authors were not totally in accordance.

Regional and local biogeographical contributions then followed (e.g. MELLO-LEITÃO 1945; VACHON 1952; KOCH 1977; FRANCKE 1978; LAMORAL 1979; COUZIJN 1981; ARMAS 1982). Most of these failed to demonstrate precise biogeographical patterns or to explain what has been called since POCOCK'S (1894) publication "apparent anomalies in the distribution of some groups of families and genera". The reasons for the inability of these authors to explain better what they observed can probably be attributed to: (i) important gaps in knowledge of the phylogeny of several of the groups studied; (ii) a rejection or an unawareness of Wegener's theory of continental drift propounded in 1912; (iii) apparent ignorance of recent theories concerning climatic vicissitudes, especially in tropical biomes, during the late Cenozoic and Pleistocene periods (these have been used successfully by other tropical biologists over the last 30 years, e.g. MOREAU 1963; PRANCE 1982*b*); (iv) major ignorance of scorpion life history strategies in the sense of MACARTHUR & WILSON (1967) and PIANKA (1970, 1988). Ecologists only started to become aware of scorpion ecology in terms of life history strategies in the late 1970s and early 1980s. This led them to classify many, if not most, scorpions as equilibrium species (POLIS 1990; LOURENÇO 1991). Until the late 1980s (LOURENÇO 1991) these new parameters for scorpion ecology remained the sole preoccupation of ecologists and were ignored by biogeographers.

A more synthetic biogeographical argument is proposed in this paper, based on UDVARDY'S (1981) division of biogeography into three spatio-temporal entities. This is largely because Udvardy's model is clear and didactic (fig. 1). In correlation with Udvardy's model three major biogeographical events may be tentatively used to explain many, or most present patterns observed today among scorpions.

I will not in this contribution try to answer all the difficult questions that have been addressed by biogeographers during the last 100 years. Because of lack of space, only a selected number of examples will be given. My main objective is to suggest to biogeographers (mainly those working with scorpions or Arachnida) the importance of clearly established historical and ecological factors in any biogeographical study.

I. PHYLOGENETIC SCALE: PALAEOBIOGEOGRAPHY

The phylogenetic scale encompasses the evolutionary time of all biota and is limited in space only by the size of the earth (UDVARDY 1981). On this scale, only historical factors can be assumed since, for almost all ecological conditions, data are largely or totally unknown. At this level, the evolutionary process of biogeography is, to a considerable extent, a tributary of continental drift and plate tectonics. This new view shook to the foundations the theories of many older paleontologists and biogeographers (UDVARDY 1981).

Both POCOCK (1894) and KRAEPELIN (1905) had made their contributions to scorpion biogeography before the Wegener's theory was propounded in 1912, while BIRULA (1917) probably ignored rather than rejected the theory. Of these authors,

POCOCK at least, in his contribution gives the impression that his intuition would have lead him accept Wegener's theory had he worked a few years later.

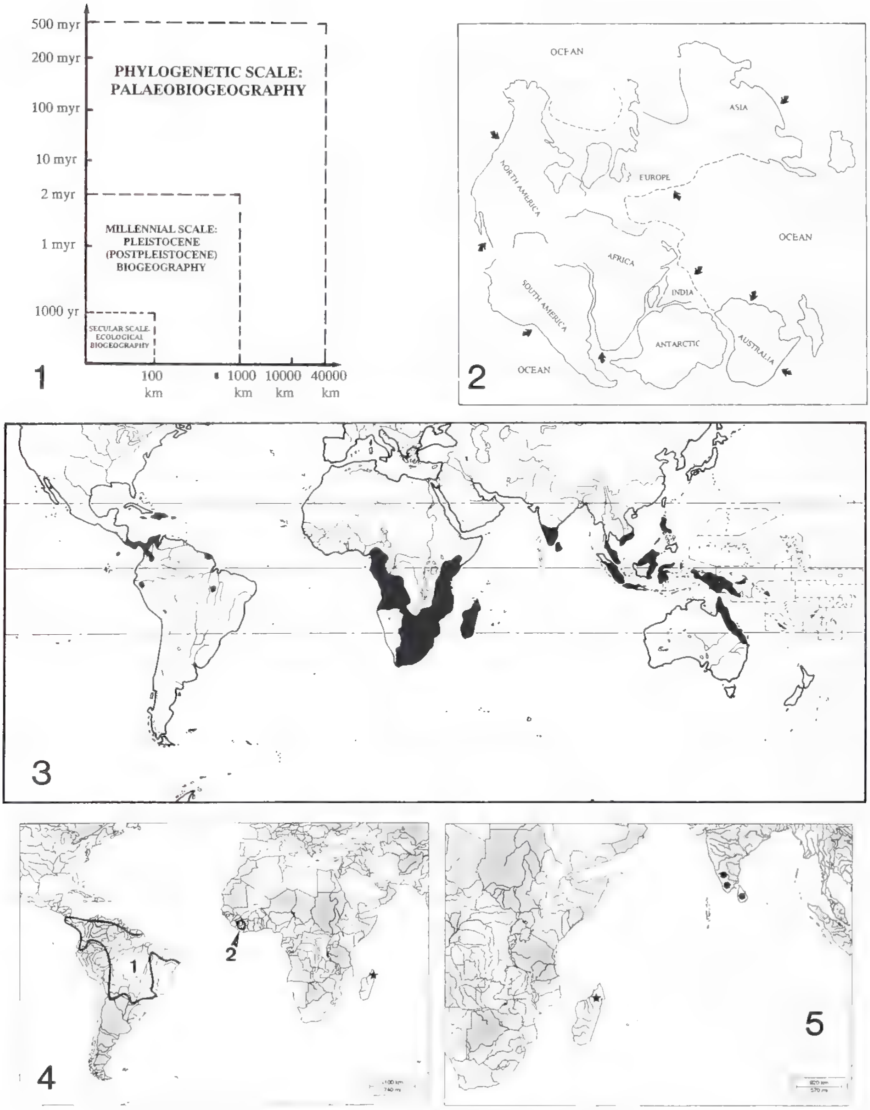
Some subsequent authors, such as MELLO-LEITÃO (1945), also ignored Wegener's theory or were too regional in their approach to take it into consideration. Others, in particular French authors (e.g., FAGE 1929; VACHON 1952; MILLOT 1948), systematically rejected continental drift. In more recent publications authors such as KOCH (1977), LAMORAL (1979, 1980) and COUZIJN (1981) have taken continental drift into consideration when discussing *ad hoc* aspects of regional biogeography[1].

LAMORAL'S (1980) suprageneric classification of recent scorpions, with its discussion of their zoogeography, remains one of the best attempts to explain the general patterns of scorpion biogeography, and was taken in consideration by SISSOM (1990). The zoogeographical suggestions which Lamoral proposes are generally acceptable, i.e., (i) the present global fauna is derived from pulmonate (Neoscorpionina) elements that originated in Laurasia and Gondwanaland during Pangean times (Fig. 2), (ii) the protobuthids were the dominant fauna during Pangean times, and the distribution of present Buthidae is the result of a vicariant process emanating from the fragmentation of Laurasia and Gondwanaland; (iii) the other protoelements, the Chaeriloids and Diplocentroids, also evolved in Laurasia and/or Gondwanaland during Pangean times. The more detailed conclusions of LAMORAL (1980) are, in one way or another, mainly correlated with vicariance and with continental drift. LAMORAL (1980) failed, however, in explaining two points. I. In my opinion he insisted too much on the role of dispersion when affirming that two major factors have influenced speciation and distribution patterns. I agree with the importance of vicariance in response to the progressive fragmentation and continental drift of Pangea and Gondwanaland, but the overland "migration" of Laurasian elements to the north of Gondwanaland needs to be reconsidered. This process of "active" dispersion should be interpreted rather as being a more "passive" process (in Haffer's 1981 dispersal sense)[2]. This opinion is supported by the poor vagility presented by modern species of scorpion[3] (Lourenço 1991). Present biogeographic patterns should be considered more as a the result of different vicariant processes, and as the pieces of an incomplete puzzle. II. Lamoral did not answer the question about "apparent anomalies in the distribution of some groups of families and genera". These "anomalies" have been discussed since the publication of POCOCK'S (1894) work. Even today the dis-

[1] A zoogeographical analysis of the world scorpion fauna, based on literature synthesis has been proposed in a recent publication (NENILIN & FET 1992). This contribution (in Russian), which was written in 1983/84 presents, however, several gaps in the bibliography. For this reason, it seems difficult to refer to this paper in the present contribution.

[2] Because of lack of space I will not discuss here the arguments of PLATNICK (1976), UDVARDY (1981) and HAFFER (1981) regarding their personal opinions about the meaning of both dispersion and dispersal (see also LOURENÇO 1986*a*).

[3] It might be suggested that primitive or aquatic scorpions were better able to disperse than terrestrial forms. They were therefore able to reach many of the shores of Pangea before and during the fragmentation process, since scorpions remained marine (or aquatic) from the Silurian until at least the Triassic (BRIGGS 1987; SHEAR & KULALOVA-PECK 1990).



FIGS 1–5

Fig. 1. Division of biogeography into the three spatio-temporal scales of Udvardy (modified after UDVARDY 1981). Fig. 2. Position of Pangea about 200 my B.P., and hypothetical ways of coastal colonisation by aquatic scorpions. Fig. 3. Gondwanian distribution (in black) of scorpions of the family Ischnuridae (cf. *Opisthacanthus*). Fig. 4. Distribution of the genus *Ananteris* in tropical America (1) and Africa (2), and of the related species of *Tityobuthus* in Madagascar (black star). Fig. 5 Distribution of *Charmus* in India and Sri Lanka (black rounds) and of *Microcharmus* in Madagascar (black star).

junct distributions of Diplocentridae and Iuridae remain unexplained. These families are found in the Neotropics and, respectively, in the Arabian and the Mediterranean regions. The presence of the genus *Opisthacanthus* in both Afrotropical and Neotropical realms was also considered as an "anomaly". The case of the two disjunctly distributed families should be regarded as a result of the previous distribution of protoelements of both families, this result being the consequence of vicariant processes. The exact mechanism of these process has not, however, yet been explained. The patchy distribution of *Opisthacanthus* was finally clarified by LOURENÇO (1985a) who presented all the necessary evidence to suggest that this genus was of typical Gondwanian lineage (Fig. 3), thus invalidating both NEWLANDS' (1973) transatlantic rafting theory and FRANCKE'S (1974) reshuffle, and clearly suggesting that elements of this genus were already present in the African and Brazilian shields of Gondwanaland prior to the continental fragmentation that took place in the second half of the Cretaceous. Further evidence for this pattern of distribution has also been produced for the genus *Ananteris* (LOURENÇO 1985*b*, 1993). A recent revision on the scorpions of Madagascar (LOURENÇO 1995) brings new evidence of Gondwanian lineages: (i) the demonstration of a close relationship between the Neotropical/ Afrotropical genus *Ananteris* and the genus *Tityobuthus* endemic to Madagascar, and (ii) the discovery of a new genus, *Microcharmus*, closely related to the genus *Charmus* from India and Sri Lanka. These results will be developed in a forthcoming paper on the biogeography of Madagascar (Figs 4 & 5).

In conclusion, I suggest that the main event responsible for determining the biogeographic patterns of scorpions on a palaeogeographic scale, has been the fragmentation of Pangea and subsequent continental drift. The difficulties in explaining the significant discontinuous distribution of the Iuridae and Diplocentridae point not only to the great geological age of most families and genera, but also to the relict faunas and biogeographical patterns which they exhibit today. In the next section I will attempt to explain regional patterns as complements to the palaeobiogeographical scale.

II. MILLENIAL SCALE: PLEISTOCENE BIOGEOGRAPHY

Since the development of the earth's crust until the Pleistocene epoch several events took place, many of which were related to the continuous drift of the continents. Without citing an exhaustive list, the following can be mentioned: mountain building, differential erosion, epicontinental seas, climatic-vegetational fluctuations, changes of world sea level and the formation of major river systems. All these events took place during the Cenozoic over a period of 60 M.Y., and have influenced the present biogeographical patterns of scorpions. In this section I will make special reference to one of these events, climatic-vegetational fluctuation, which played a major role since the late Cenozoic and which has had a major impact during Pleistocene times[4]. For more details of the consequences of the other events, refer to HAFFER (1981).

[4] For a better understand of the astronomical basis of the climatic oscillations – "Milankovitch cycles" – see HAFFER 1993.

For many years, books and papers about the tropical regions, and in particular about Amazonia, have stated that the biogeographical and diversity patterns observed in these regions could be explained by the long stability of tropical forests over millions of years (FEDEROV 1966; RICHARDS 1969). Subsequent work on geology, paleoclimates and palynology, especially in Amazonia (PRANCE 1982*a*), has demonstrated that this presumed stability was a fallacy. In fact, although the temperatures in tropical lowlands remained "tropical" during glacial periods (3–5°C lower than today), the forest broke into isolated remnants during cool dry periods (glacial phases). The remnants of forest expanded and coalesced during warm humid periods (interglacial phases). Conversely, nonforest vegetation expanded during glacials and retreated during interglacial phases (as at present). Data from geoscience have been insufficient to indicate the precise areas of changing forests and nonforests and, in particular, the areas in which forests remained during arid phases, presumably serving as refugia for animal and plant populations. Biogeographical studies of neotropical plants and animals indicate several centers of species endemism which are separated by zones of overlap and interbreeding (see PRANCE 1982*a*). More recent studies on the biogeographical patterns of the Amazonian scorpions (LOURENÇO 1986*b*, 1987) led to the definition of several endemic centers which are well correlated with the results of PRANCE (1982*b*) on woody plants, and HAFFER (1969) on birds (Fig. 6).

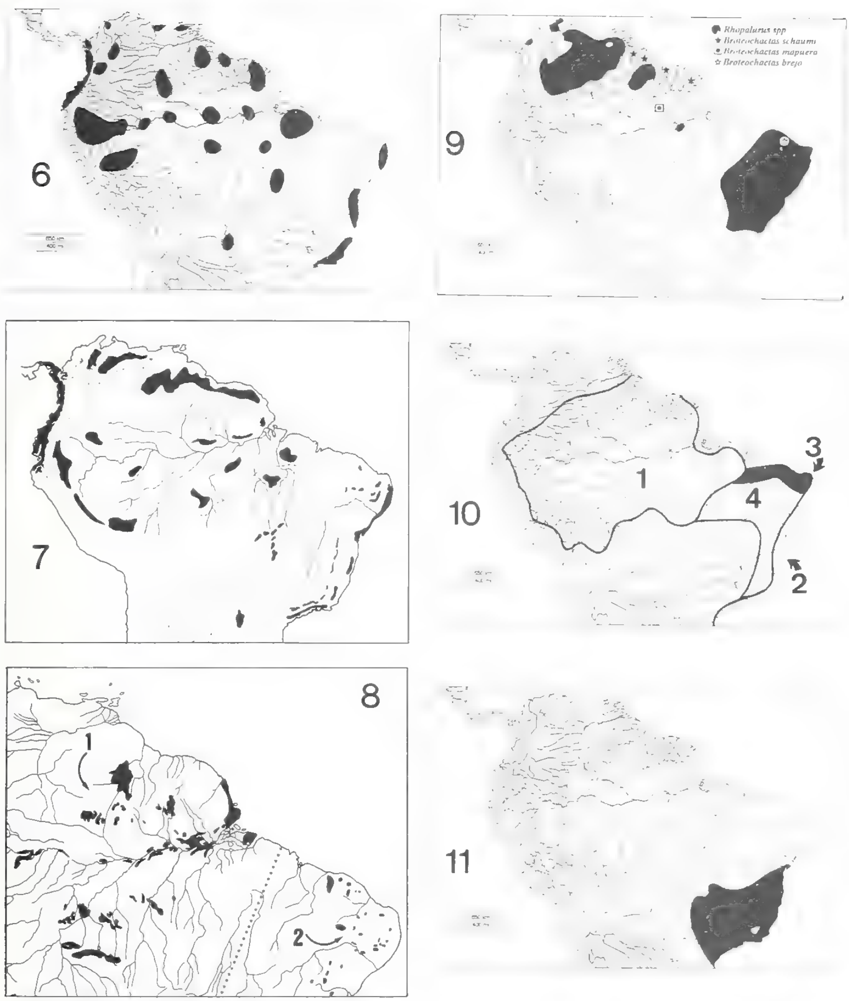
Two biogeographical patterns observed in neotropical scorpions clearly suggest direct correlations with climatic-vegetational fluctuations during the Pleistocene.

(i) Polymorphic species in the Amazon region

Tityus gasci Lourenço and *Tityus silvestris* Pocock have distributions ranging from French Guyana to Peru and Ecuador. Analysis of the variability of patterns of pigmentation and morphometric values in both species indicates a gradual geographic cline along a transect for *T. gasci*. This species was defined as a clinally polymorphic species, whereas considerable variation which was not well correlated geographically was observed for *T. silvestris* (LOURENÇO 1988; 1994). This type of pattern was first encountered by botanists, and species showing it are termed "ochlospecies"[5] (PRANCE 1982*b*). According to PRANCE (1982*b*), ochlospecies are common in many large genera of plants (> 100 species) – *Tityus* has about 120/130 species. Prance suggests that during the dry periods of the paleoclimatic episodes when the forest was reduced to small patches, widespread species became fragmented into several isolated allopatric populations. These isolated populations of ecologically adaptable species (which is the case with some *Tityus* spp.) rapidly recolonized the reestablished forest during wet episodes. Previously isolated populations thereby became contiguous. Temporary reproductive isolation did not produce genetic barriers (at least for woody-plant and scorpions) and only minor morphological differences evolved. Where species reunited the variation was no longer correlated geographically[6].

[5] From the Greek – *ochlos* = mob + species.

[6] The complex biogeographic patterns observed in several Saharo-Sindian genera of scorpions (VACHON & KINZELBACH 1987), could tentatively be explained in the light of late Cenozoic vicissitudes of the biomes extending from Morocco to India.



FIGS 6–11

Fig. 6. Tropical South America centers of endemism, defined after scorpion distribution patterns. Fig. 7. Hypothetical distribution of forests (black areas) and savannas (white areas) in tropical South America during cool dry periods (modified after AB'SABER 1977). Fig. 8. Distribution of enclaves of savanna inside Amazonia (black areas indicated by 1) and forested islands inside xerophytic formations (black areas indicated by 2). Fig. 9. Examples of disjunct distribution of genera and species in forest and savanna formations. Fig. 10. Relationship between the Atlantic and Amazon forests. 1 and 2 are the present distribution of the Amazon and Atlantic forests. 3 = suggested paleodistribution (strong evidence). 4. suggested paleodistribution (weaker evidence) (modified from BIGARELLA & ANDRADE-LIMA 1982). Fig. 11. Present distribution range of *Tityus serrulatus* in Brazil (black area) over disturbed environments and, suggested original area of distribution (small white area inside black area) prior to recent anthropic influences.

(ii) Disjunct distributions of scorpion taxa in savanna and rainforest formations

Examples of genera presenting a discontinous distribution are provided by scorpions which are exclusively adapted to savannas (*Rhopalurus* spp.) or to rainforests (*Broteochactas* spp.). *Rhopalurus amazonicus* Lourenço is endemic to an enclave of savanna inside the Amazonian rainforest (Fig. 8) whereas *Broteochactas brejo* Lourenço is found only in a forested island inside arid formations of northeast of Brazil (Fig. 8). These isolated endemic populations provide good evidence for the hypothesis of past connections between the savannas of central Brazil and present enclaves in Amazonia and Guayana (Fig. 9). During past dry periods the savanna formations probably coalesced (Fig. 7). The presence of enclaves of forest (brejos) inside arid formations (Fig. 8) suggests past connections between Amazonia and the Atlantic forest of Brazil (Fig. 10). This hypothesis is supported by the biogeographical pattern in Amazonia presented by scorpions of the genus *Broteochactas* and by the Chactinae in general (Fig. 9).

III. SECULAR SCALE: Ecological biogeography

The analysis of responsible ecological factors in the explanation of the biogeographic patterns of scorpions have been biased for two major reasons: (i) there has been an almost total lack of knowledge of life history strategies until about 15 years ago – knowledge which, until the late 1980s, was almost the only preoccupation of ecologists, and (ii) a generalized opinion, even among modern biologists, according to which scorpions are ecologically plastic organisms capable of withstanding radical changes in environmental conditions, and therefore of being very good colonisers. This second assumption is a fallacy. With our growing knowledge of scorpion life history strategies it can be seen that many if not most scorpions are undoubtdly equilibrium species which tend to inhabit stable and predictable natural environments, produce single egg clutches, do not store sperm, have long life-spans, present low population densities, have a very low r_{max}, show weak mobility, and are highly endemic, often known from a single locality.

In contrast some scorpions are opportunistic species, such as certain members of the genera *Centruroides*, *Tityus* and *Isometrus*. These exhibit marked ecological plasticity and are readily capable of invading disturbed environments. They produce multiple clutches from a single insemination, have elaborate sperm storage capabilities (Kovoor *et al.* 1987), short embryonic development, short life spans, high population densities, rapid mobility, and are widely distributed. These opportunistic species are of little use for establishing biogeographical patterns, although fortunately they can readily be identified and disregarded.

Opportunistic species evolve mainly in disturbed and unpredictable environments which are the result of natural (e.g. volcanic activity) or anthropic action. Long known examples include the presence of a population of the neotropical species *Centruroides gracilis* (Latreille) in the Canary Islands (Kraepelin 1905; Lourenço 1991) and the worldwide distribution of the Indo-Malayan scorpion *Isometrus*

maculatus (DeGeer) which has been transported by human agency during the last four centuries and is today present in almost all tropical coastal regions. Some elements have even been found at a distance of 3000 km upstream of the delta of the River Amazon (Lourenço 1991). The phenomenon of the replacement of species is well illustrated in several islands of the Caribbean, where natural volcanic activity and human impact are important. In this region, many endemic populations of equilibrium species are regressing or have disappeared, to be replaced by opportunistic species of the genus *Centruroides* which now occupy most of the Islands (Lourenço 1992).

In continental regions, opportunistic species can rapidly occupy habitats disturbed by human activities, where the original native species have been selected against, thus leaving their ecological niches vacant. This kind of situation can be observed in Brazil and Mexico where very dense populations of species as *Tityus serrulatus* Lutz & Mello and *Centruroides suffusus* Pocock, respectively, occupy large geographic areas. When this phenomen of secondary succession is associated with noxious, opportunistic species, public health problems can arise (Lourenço & Cuellar 1995; Lourenço & Cloudsley-Thompson 1996).

CONCLUSIONS

Although the presence of a reduced number of opportunistic scorpion species may not be a good indication of predictable biogeographic patterns, many or most scorpions are equilibrium species and can be useful models in biogeographical research. Several factors make scorpions useful for biogeographical (or biodiversity) studies, as suggested by Noss (1990): (i) stabile taxonomy, at least for some regions of the world; (ii) life history strategies that are well understood; (iii) the fact that individuals can readily be observed in the field with the use of UV light, and (iv) biogeographical and endemic patterns that are well correlated with those of other taxa of animals and plants (see Lourenço 1987). Scorpion biogeographers, however, need to be more aware, in their interpretations, of the distinction between the historical and the ecological factors responsible for the biogeographical patterns observed.

In conclusion, the definition of biogeographical (or biodiversity) patterns is a matter for specialists. The number of experienced specialists is drastically decreasing in many countries mostly because of lack of interest from governmental and academic authorities. The time required for the adequate training of students in evolutionary biogeography is long – up to 10 or 15 years. In consequence, this situation threatens to generate important gaps in this discipline (Lourenço & Blanc 1994).

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The evolutionary significance of colour, colour patterns and fluorescence in scorpions

Wilson R. LOURENÇO* & John L. CLOUDSLEY-THOMPSON**
* Laboratoire de Zoologie (Arthropodes), M.N.H.N., 61 rue de Buffon, F-75005 Paris, France.
** Department of Biology, University College London, Gower Street, London WC1E 6BT, United Kingdom.

The evolutionary significance of colour, colour patterns and fluorescence in scorpions. - From a survey of the scorpion faunas of North Africa, Namibia, Baja California, tropical South America and the Caribbean, it is concluded that the principal function of the colour of scorpions is crypsis – pale or variegated in open savanna and deserts, dark in dense vegetation and rain-forest. Probable explanations are given for the existence of species that are exceptions to this rule. The possible functions of fluorescence in ultra-violet light are also discussed.

Key-words: Scorpion - colour - colour patterns - crypsis - fluorescence - ultra-violet light.

INTRODUCTION

The colour and colour patterns of scorpions have often attracted the attention of biologists, mostly in relation to taxonomic studies (e.g. Kraepelin 1899; Pocock 1902; Vachon 1952; Lourenço 1980; Lamoral 1979). The ecological significance of colours and patterns are, however, much less well understood (Cloudsley-Thompson 1993*a*, *b*). Moreover, biologists have long disregarded the importance of ontogenic variability in colours and colour patterns. This leads to errors in the definition both of species and of natural populations. Only recently has this point begun to be elucidated (Lourenço 1980, 1983), and it is now realized that, in many species, juveniles and adults have totally different colour patterns. The coloration of scorpions ranges from almost black to very pale yellow, while some troglobitic species such as *Sotanochactas elliotti* (Mitchell), are almost totally unpigmented.

According to Cloudsley-Thompson (1961, 1993*a*, *b*), scorpions may have evolved nocturnal behaviour patterns in response to predation. Moreover, it is gene-

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rally assumed that their colours and colour patterns are nearly always associated with crypsis (POLIS 1990; CLOUDSLEY-THOMPSON 1993*a*, *b*). Thus, most of the scorpions that live in open areas such as deserts and dry savannas are pale, whereas those living in dense vegetation and rain-forests are dark and often black.

A question arises, however, as to why several exceptions to this rule can be observed. The object of our paper is to answer this question at least partially. We base our arguments on examples from well studied faunistic regions such as North Africa, Namibia, Baja California, tropical South America and the Caribbean.

Another characteristic of scorpions, which is shared with other orders of Arachnida, is the emission of a fluorescent glow when exposed to ultra-violet light. This has been demonstrated in numerous species belonging to all families (CLOUDSLEY-THOMPSON 1978) but its function is little understood. This phenomenon, too, will be discussed in the present paper.

I – EXAMPLES FROM DESERT FAUNAS

Most of the species present in desert regions are pale yellow and unpigmented. Exceptions can, however, be found. For example, in the North African deserts, most varieties of *Scorpio maurus* (Linnaeus) are dark, which is in accordance with the general coloration of the family Scorpionidae. Among Buthid scorpions, species such as *Orthochirus innesi* Simon, *Hottentotta franzwerneri* (Birula), *Buthus maroccanus* Birula and *Microbuthus fagei* Vachon, show dark pigmentation. The same applies to species of the genus *Butheoloides* Hirst. In this case, however, only one species, *Butheoloides maroccanus* Hirst, lives in truly desert areas.

Another marked exception is found in the genus *Androctonus* which presents several dark coloured species, *A. hoggarensis* (Pallary), *A. aeneas* Koch, *A. crassicauda* (Olivier), *A. mauretanicus* (Pocock) and *A. sergenti* Vachon, whereas only two are pale yellow, *Androctonus australis* (Linnaeus) and *A. amoreuxi* (Aud. & Sav.). Other species from North Africa, which belong to the genera *Buthacus*, *Cicileus*, *Buthiscus*, *Lissothus*, *Leiurus*, *Compsobutulus* and *Buthus*, are all pale (VACHON 1952).

In other desert regions, such as Saudi Arabia and Oman (VACHON 1977, 1979), the scorpions are also usually pale in colour. The same exceptions occur there in species of *Androctonus*, and in *Orthochirus innesi* but even Scorpionidae such as *Hemiscorpius arabicus* Pocock, *Hemiscorpius maindroni* Simon and *Scorpio maurus kruglovi* Birula are lighter in colour than in North Africa and are dark yellow.

In Namibia, a dichotomy associated with colour pattern and phylogenetic relationship is to be observed even more clearly. Buthidae of the genera *Hottentotta*, *Karasbergia*, *Parabuthus* and *Uroplectes* are, in general pale, whereas the Scorpionidae are dark. An exception in the last family is *Hadogenes phyllodes* (Thorell) which is paler than the other species (LAMORAL 1979).

In the North American deserts, and especially in Baja California, species of Buthidae and Vaejovidae are pale, whereas these of Diplocentridae are rather dark. Some exceptions are *Hadrurus pinteri* Stahnke, *Nullibrotheas allenii* Wood, *Vaejovis*

gigantaensis Williams, *Vaejovis harbisoni* Williams and *Vaejovis janssi* Williams which are dark (WILLIAMS 1980). Finally, in the arid regions of Australia, species belonging to the genus *Urodacus* (Scorpionidae), are pale yellow (KOCH 1977).

II — EXAMPLES FROM OPEN VEGETATION FORMATION FAUNAS

Some of the formations of open vegetation best studied are those of the South American savannas, i.e. Chaco, Cerrados and Llanos, and those of arid South America such as the Caatingas in North East Brazil (LOURENÇO 1982, 1990*a*, 1994; LOURENÇO & EICKSTEDT 1988). The scorpion faunas of the African savannas are less well known and still present many gaps in knowledge (LOURENÇO & SASTRE 1988). For this reason, in the present paper, examples have been cited mainly from South America.

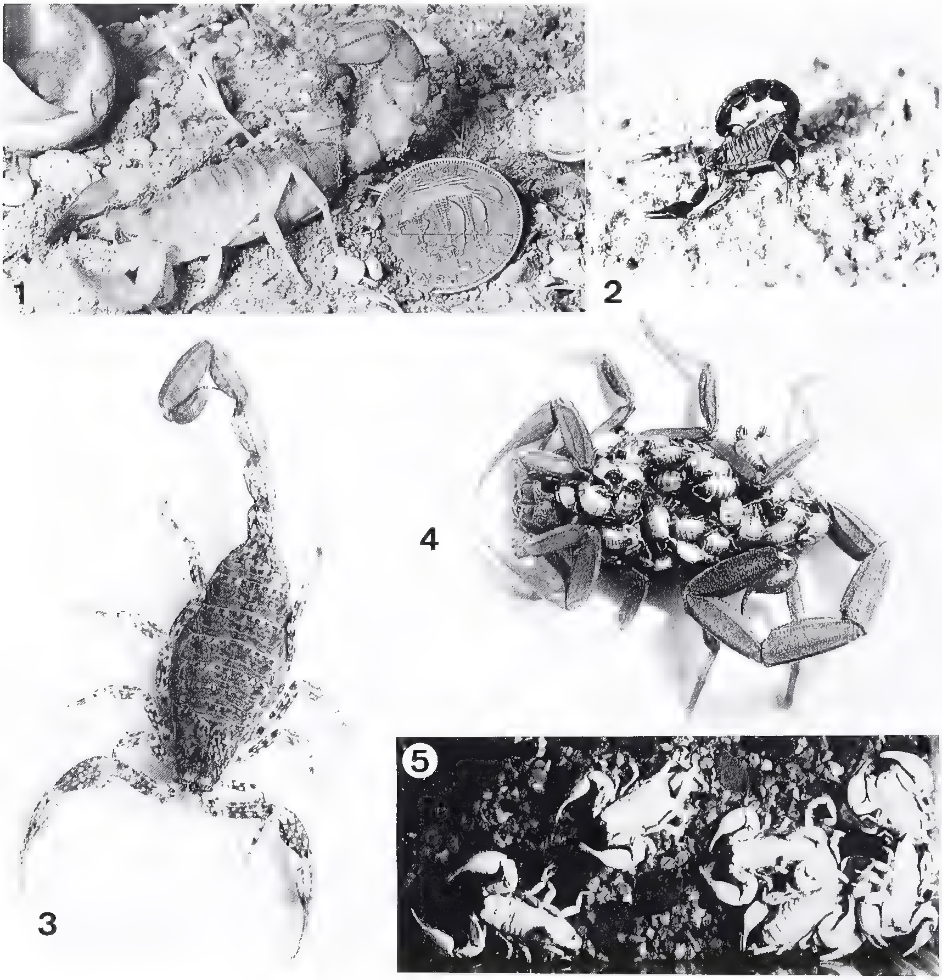
Only two scorpion families, the Bothriuridae and the Buthidae, are present in the region lying between the North of Argentina, and North East Brazil. This includes Paraguay and the Central region of Brazil and is known as "the diagonal of Brazilian open formations" (DE MARTONNE 1935; LOURENÇO 1990*a*). Almost all the species of Buthidae found here are pale, whereas those of the Bothriuridae are usually dark. Some exceptions occur in both cases, however. Thus, of the Buthids, *Rhopalurus acromelas* Lutz & Mello-Leitão and *Tityus bahiensis* (Perty) are rather dark while, of the Bothriuridae, *Bothriurus rochai* Mello-Leitão and *Brachistosternus (M.) ferrugineus* (Thorell) are pale.

All species of *Rhopalurus* are adapted exclusively to open vegetation. Their colour ranges from yellow in *Rhopalurus rochae* Borelli to brown-yellow in *Rhopalurus agamemnon* (Koch). Even *Rhopalurus amazonicus* Lourenço, which lives in patchy areas of savanna enclave within the Amazonian rain forest, is yellow (LOURENÇO 1982*a*, 1986).

The species of *Tityus* living in open vegetation show two major types of coloration. In the first there are species ranging from yellow, as *Tityus stigmurus* (Thorell) or reddish-yellow, as *Tityus trivittatus* Kraepelin, grading into brown-yellow as in *Tityus fasciolatus* Pessôa. In the second group, a dark variegated colour pattern is found over a yellow or a clear colour base. This pattern, which can be observed in species such as *Tityus paraguayensis* Kraepelin and *Tityus mattogrossensis* Borelli, is also present in the other species of *Tityus* belonging to the same phylogenetic group and living in dry areas or rain forest (LOURENÇO 1992). We will discuss this further below. A similar pattern is also to be seen in species of the genera *Ananteris* and *Microtityus* which likewise inhabit both open and forested regions (LOURENÇO 1982*b*; LOURENÇO & EICKSTEDT 1983).

III – EXAMPLES FROM FOREST FAUNAS

The scorpions of the forest ecobiome are generally dark brown or black. This is the case in species of the families Scorpionidae, Ischnuridae, Chactidae, Chaerilidae, Diplocentridae and Buthidae. Few examples of pale species can be found

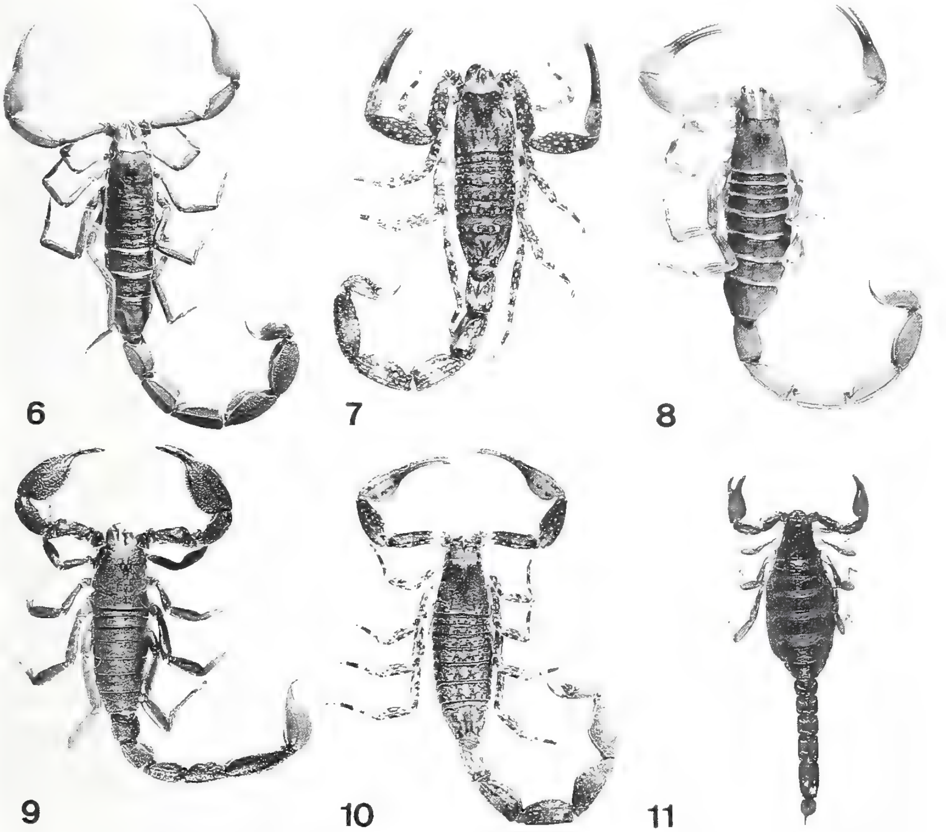


Figs 1–5

Fig. 1. *Androctonus australis* an yellow scorpion from desert regions of North Africa. Fig. 2. *Androctonus crassicauda* a dark scorpion from desert regions of North Africa and Middle East. Fig. 3. *Tityus mattogrossensis*, a variegated scorpion from Brazilian Savannas. Fig. 4. *Centruroides gracilis* a dark scorpion from both dry savannas and forests from the U.S.A. to South America. Fig. 5. *Opisthacanthus cayaporum* a dark scorpion from Brazilian Savannas, under ultra-violet light.

in the first two families. *Opisthacanthus valerioi* Lourenço, from Cocos Island is one of the exceptions, as it is yellow. Some other instances occur in Africa both of Scorpionidae and Ischnuridae with dark yellow-brown coloration.

Species of Chactidae (at least of Chactinae), living in forests, are uniformly dark probably as an adaptation to the vegetation. *Chactas keyserlingi* Pocock, which



FIGS 6–11

Fig. 6. *Tityus metuendus*, a black scorpions from Amazonia. Fig. 7. *Tityus metuendus*, juvenile with a characteristic variegated colour. Fig. 8. *Tityus raquelae*, a pale scorpion from Amazonia. Fig. 9. *Brotheas amazonicus* a dark scorpion from Amazonia. Fig. 10. *Tityus silvestris*, a variegated scorpion from Amazonia. Fig. 11. *Bothriurus araguayae* a dark scorpion from Brazilian Savannas.

is found in arid regions of Colombia; is the only known example of a species of Chactinae living in an arid region, but this species is also dark (LOURENÇO 1991).

Species of the families Chaerilidae and Diplocentridae, are usually red-brown to dark-brown. They can be found in both open vegetation and forested regions. Species of Buthidae living in forests are almost invariably dark brown or black; for example, several *Tityus* and *Centruroides* spp. of South, Central and North America. A common colour pattern, variegated dark brown over a pale base, is to be seen in species of open vegetation. This pattern is very common among species of the genera *Ananteris* and *Microtityus* in the Neotropics, as well as in species of the genera *Isometrus* and *Lychas* in Africa, the Indo-Malasyan region and Australia. Moreover,

the same pattern is also seen in the juvenile forms of both *Tityus* and *Centruroides* spp. that are dark brown or black when adult (Lourenço 1983). We shall return to this point in the Discussion.

Several interesting exceptions, provided by species of *Tityus* and *Centruroides* living in forests in South and Central America, can be listed: *Tityus engelkei* Pocock from Santa Marta in Colombia is yellow. *Tityus sastrei* Lourenço & Florez and *Centruroides margaritatus* from Pacific coastal forests in Colombia and Ecuador are yellow-red to yellow-brown. *Tityus gasci* Lourenço, *Tityus blanci* Lourenço, *Tityus strandi* Werner, *Tityus jussarae* Lourenço (this is a trogloxene species), *Tityus melanostictus* Pocock, *Tityus discrepans* Pocock and *Tityus filodendron* Gonzalez-Sponga, from the Amazonian region, are mostly yellow or sometimes reddish-yellow.

In other forests such as the Atlantic coastal forest of Brazil, no pale or yellow species are known. The colours and patterns are invariably dark brown, black or variegated, as in *Tityus brazilae* Lourenço & Eickstedt and *Tityus pusillus* Pocock. African, Asian and Australian forests providing examples of pale species are poorly known, but it is certain that exceptions, such *Hottentota hottentota* (Fabricius), which are found both in arid regions and tropical forest, are also present there.

FLUORESCENCE IN ULTRA-VIOLET LIGHT

It has long been known that scorpions fluoresce very strongly when exposed to ultra-violet light in the range 320–400 nm (3.200–4000 Å), which facilitates their study and collection in the field (SISSOM *et al.* 1990). Fluorescence in ultra-violet light also occurs with other Arachnida (and other Arthropoda), especially Solifugae, but its significance in not understood (CLOUDSLEY-THOMPSON 1978). It gradually fades when scorpions are maintained continuously in ultra-violet light and, after about a week, disappears entirely. If a piece of black adhesive tape has first been attached to the opisthosoma of a scorpion, after it has lost the ability to fluoresce only that portion of the body which had previously been covered will show fluorescence when the tape is removed. The reaction occurs in the hyaline exocuticle and the substance which causes fluorescence is soluble in alcohol: it can be crystallised out (C. Constantinou, *in litt.*). Water loss in dry air at 23°C from an adult living *Androctonus crassicauda* (Olivier) doubled over a period of 15 days when the scorpion was maintained under ultra-violet light (700 μW cm^{-2}) in the laboratory (CONSTANTINOU & CLOUDSLEY-THOMPSON 1985).

Fluorescence in ultra-violet light is known for only a small number of day-active Arachnida including spiders (LOURENÇO *et al.* 1988; LOURENÇO 1990*b*), while new-born scorpions do not fluoresce until their cuticle has sclerotized. According to F.H. Koehler (cited by HJELLE 1990), it may be possible for a scorpion to detect very low intensities of light at certain wavelengths. This may explain the extreme sensitivity to light of the eyes of *Androctonus australis* (L.) reported by FLEISSNER & FLEISSNER (1985). In any case, there is no evidence to show that scorpions react to one another visually, either when mating or when one individual preys upon another. We

doubt whether the basic function of the fluorescent chemical is waterproofing, or that it makes scorpions attractive to insect prey. It is possible, however, that in daylight scorpions could absorb a degree of radiation that might have a deleterious effect upon the cuticles, just as sunlight does on many man-made polymers (CLOUDSLEY-THOMPSON 1978).

DISCUSSION

From the examples presented above, it seems logical to suggest that the colours and colour patterns of scorpions have a primarily cryptic significance. They seem also to be associated with phylogenetic lineage. The species of Chactidae (at least of Chactinae), as well as of most Scorpionidae and most Diplocentridae, are dark, regardless of the habitat in which they live. It is reasonable to assume that a dark colour is cryptic in forests and dense vegetation, and that pale colours and yellow are cryptic in deserts and open vegetation. However, the third type of coloration observed, variegated colours, seems to be effective in both forests and open vegetation since species presenting this pattern occur in both. Moreover, the juveniles of black species such as *Tityus cambridgei* Pocock, *Tityus metuendus* Pocock and *Centruroides gracilis* (Latreille), show a variegated pattern almost until they became adult. Variegated colours probably act as camouflage: They are not found in desert species.

What possible explanation can be given for the presence of dark species in deserts and of pale or yellow species in forests? Most lineages of scorpions are very old (SISSOM 1990), and colour patterns have been established in different taxa over a very long period of time. The evolution of these colours is undoubtedly associated with the ecological requirements of the environment. It is possible that scorpion species will naturally evolve dark or pale colours in a given amount of time, which is not necessarily short. The colours and patterns observed today probably evolved at moments of paleohistory when different environments experienced long periods of stability (most existing scorpion groups had undoubtedly evolved before the Cenozoic). In more recent times, especially during the Pleistocene and Holocene, rain-forests and savannas experienced considerable vicissitudes in their climatological conditions. Several periods of expansion and contraction, both of rain-forests and of arid savannas, are known to have occured in Amazonia during the Pleistocene and Holocene (HAFFER 1969; PRANCE 1982, 1985; LOURENÇO 1987).

According to PRANCE (1982, 1985), the reduction of forest to small patches affected the organisms existing there in one of three ways: *(a)* they became extinct; *(b)* they survived with little or no evolutionary changes, or; *(c)* they began to differentiate and even to speciate in refugia. It seems logical to assume that situations *(a)* and *(b)* took place most frequently. Black species therefore remained in forested refugia: when the forest expanded again, they merely recolonised the whole environment. On the other hand, during periods of forest expansion, some pale species, which had previously colonised dry savanna formations, may possibly have evolved rapidly in terms of their behaviour and physiology so that they were able to survive in a forested environment.

This rapid evolution was not followed by any modification of colour, which probably takes much longer. It is possible that pale forest species may be less well adapted in terms of crypsis, and that they may suffer negative selection by predators. However, scorpions are nocturnal, and even if forest species are much less nocturnal in their activity than are desert species (CLOUDSLEY-THOMPSON 1981), forests are so dark that this vegetation and deserts, a possible readaptation from a previously forested environment may also be the explanation. However, in this case they would be much more exposed to predation because they lack cryptic protection unless, of course, the dark coloration is aposematic under these conditions (CLOUDSLEY-THOMPSON 1993*a*, *b*).

The different examples of coloration in scorpions presented in this paper are not exhaustive. Our object has been to try to explain the significance of coloration and pattern, and the causes of some of the exceptions to the general principles proposed. We have been less successful in attempting to explain the function of fluorescence in ultra-violet light.

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The Australian funnel-web spider: overkill or coevolution?

Barbara York MAIN
Zoology Department,
University of Western Australia, Nedlands, Western Australia 6009, Australia.

The Australian funnel-web spider: overkill or coevolution? - The Australian funnel-web spiders *Atrax* and *Hadronyche* are amongst the most venomous spiders in the world. Curiously although toxic to humans and monkeys the spiders are not poisonous to certain other warm blooded vertebrates. The natural prey of the spiders while comprising mainly insects and other invertebrates also includes cold blooded vertebrates such as indiginous frogs and lizards. It is proposed that the venom has become highly toxic as a result of coevolution between the spider and a natural predator. Antecedents of the contemporary bandicoots (Peramelidae) which lived in the same habitats as the funnel-web spiders are suggested as the most likely coevolutionary sparring partners. In accordance with a coevolutionary hypothesis the funnel-web venom could have developed as a defence against such predators. As background for this hypothesis, the systematic relationships, distribution, habitat, prey and possible predators of the spiders are discussed in the context of historical ecology and present-day biology.

Key-words: Funnel-web spiders - *Atrax* - *Hadronyche* - venomous spiders - bandicoots (Peramelidae) - coevolution - Australia.

INTRODUCTION

Spiders feed predominantly on invertebrates and arthropods comprise their main diet. However, some spiders from widely disparate taxa are known to occasionally capture and feed on vertebrates. Cold blooded vertebrates e.g. lizards, snakes and frogs and even acquatic forms such as small fish and tadpoles and warm blooded vertebrates including house mice and birds have all been recorded many times as falling prey to the following range of hunting and sit-and-wait spiders: huntsman spiders (Heteropodidae), pisaurids (*Dolomedes* species), various trapdoor, funnel-web and other mygalomorph spiders as well as webweavers particularly Theridiidae and

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Araneidae (e.g. early records include BATES 1884; EWING 1933; GERTSCH 1949; LAWRENCE 1964). Vertebrate prey is suppressed promptly by venom or a combination of web-wrapping and venom or possibly in some cases simply by silk entanglement and wrapping.

Several Australian spiders, notably the theridiid redback spider (*Latrodectus hasselti*), araneid orbweavers such as *Nephila*, the pisaurid *Dolomedes* and various mygalomorphs e.g. *Selenotypus plumipes*, *Selenocosmia* species, *Aganippe rhaphiduca* and possibly *A. subtristis* as well as at least two funnel-web spiders e.g. *Atrax robustus* and *Hadronyche formidabilis* are known to feed at least occasionally on vertebrates. The list of such prey includes fish, frogs, tadpoles, lizards, snakes, house mice and chickens, bats and small birds. MCKEOWN (1963) graphically described some instances and RAVEN (1988) summarised most of the references. In addition KÖNIG (1987) recorded a gecko and A. Wells (pers. comm.) photographed a snake, in each instance as web-trussed prey of the redback spider. CLIFFORD (1988) noted *Achaearanea tepidariorum* feeding on skinks and I have observed a snake, lizard and frog amongst the prey of the large trapdoor spider *Anidiops* (= *Gaius*) *villosus*.

Apart from the aggressive predation on fish and tadpoles by *Dolomedes*, it would seem that vertebrate captures are fortuitous. In most cases spiders subdue such prey through a combination of web-wrapping (usual behaviour for araneids and theridiids) and venom injection (by theridiids). Subjection of vertebrates by *Dolomedes* and mygalomorphs is probably first by physically restraining the prey and then by venom injection.

Encounters with large vertebrates sometimes results in serious envenomation. In addition to human indisposition and fatalities from redback and funnel-web spider bites there is in Australia at least one instance of mortality of another warm blooded vertebrate (a dog) due to mygalomorph venom (*Selenocosmia stirlingi*) (ROBINSON & GRIFFIN 1983).

Adaptive direction and evolution of toxicity to vertebrates of spider venom

The question arises why are certain spiders, whose diet comprises essentially invertebrates, lethal or at least toxic to vertebrates including humans? [Conversely there is the anomaly that the toxin of *Dolomedes*, which often feeds on aquatic vertebrates, is apparently lethal to fish and tadpoles (cold blooded vertebrates) but is not serious for humans (BETTINI & BRIGNOLI 1978)].

I will address here only the first question. Notorious examples are the relatively "timid" spiders, the wandering *Loxosceles* and the web-ensnaring *Latrodectus*, both essentially predators of invertebrates and primarily arthropods, that are nevertheless highly toxic to vertebrates. Is their venom "unnecessarily" potent? At least in the case of *Latrodectus* I would suggest that it is not but that the potency of the venom has increased due to ancillary selection to that of killing "natural" prey i.e. it is probably, perhaps secondarily, a defence against its own predators or parasites. This hypothesis is supported by circumstantial evidence that a species of *Latrodectus* (*L.*

tredecimguttatus) has non-toxic mimics. In certain stony habitats of southern Europe frequented by this species there also occurs a species of pill bug and a pill millipede (the latter a non "offensive" species) both of which are black with red spots and when "rolled up" closely resemble the abdomen of the malmignatte spider (LEVI 1965). LEVI suggested that this apparent mimicry may protect the pill bugs and millipedes from predation by species of the lizard *Lacerta* which is known to feed on other isopods

When noting the toxicity of spiders we tend to take an anthropomorphic viewpoint. Evenso, of the rich and diverse spider fauna of the world only about a dozen species from six genera are identified as being lethal to humans (BUCHERL 1971) e.g. *Atrax* (emended here to include *Hadronyche*), *Harpactirella*, *Loxosceles*, *Latrodectus*, *Lycosa* and *Phoneutria*. But clearly selection for potent venom in many spiders including funnel-web spiders has nothing to do with association with primates. GRAY (1992) remarked that the venom of spiders such as *Latrodectus* and funnel-webs comprises a "chemical cock-tail" that "enables [the] spiders to poison a diverse spectrum of normal prey" and that the venom molecules responsible for envenomation of humans are not those that kill their normal prey. Are then these other toxins indeed evolutionary accidents, extraneous to selection for prey-killing venoms or have they also been selected for as contributing some other advantage?

In that the prey of funnel-web spiders comprises mainly invertebrates and only occasionally frogs and lizards it seems logical to consider that the highly toxic venom has developed as a defence in response to a vertebrate predator. Thus the hypothesis presented here is that the venom of funnel-web spiders has been selected for (at least secondarily) in relation to defence against a natural predator. The contemporary "bandicoots" (small rat-like marsupials of the family Peramelidae) of eastern Australia are likely sparring partners today, in that they occur in the same habitat as funnel-web spiders. Historically, selection of a potent venom may have been encouraged by confrontation of funnel-web spiders with antecedents amongst the perameloid marsupials. I will outline here a hypothetical scenario which could account for the toxicity of the Australian funnel-web spiders. My approach is that of a biologist whereas to date research on the venom has been firstly from a medical (or purely biochemical) orientation and secondly all experimental work has been done on introduced exotic species.

FUNNEL-WEB SPIDERS

Taxonomic position. Two genera of "funnel-web" spiders *Hadronyche* L. Koch and *Atrax* 0. P.-Cambridge are currently recognised (MAIN 1985, GRAY 1988) and are attributed to the subfamily Atracinae by GRAY (1988), who recognised 13 of the described species as valid and together with undescribed species indicated that there are 35 identifiable species, three in *Atrax* and 32 in *Hadronyche*. Biochemical studies on the venom have generally not considered the generic distinction and have referred all species to "*Atrax*".

Affinity of the genera to other taxa is unclear. RAVEN (1985) placed *Atrax* (in which he included *Hadronyche*) close to the New Zealand *Porrhothele* Simon and more wide spread *Macrothele* Ausserer, wheras Gray (1988) accepted on zoogeographic grounds some affinity with *Porrhothele* but not with *Macrothele*. Nevertheless, the relationship appears tenuous and the two Australian genera appear to occupy a uniquely anomalous taxonomic position. In that they have no recognisable close affinity with taxa outside Australia it is reasonable to think of them as ancient, relictual genera.

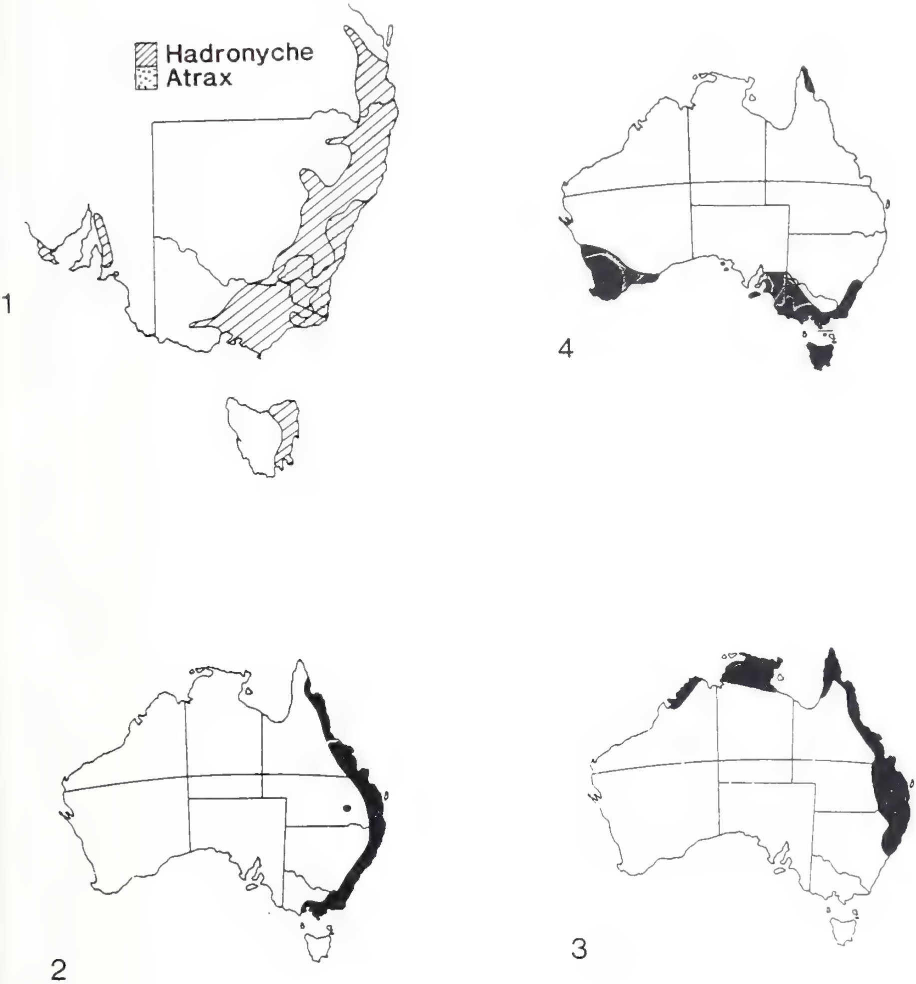
Of the two atracine genera GRAY (1988) regards *Atrax* as the more plesiomorphic genus which also fits the more uniform, conservative behaviour of the included species whereas *Hadronyche* exhibits a greater range of behavioural repertoires.

Biology and distribution. GRAY (1987, 1988) outlines the distribution patterns of the atracine species. Briefly the overall distribution as recorded for the two genera extends from the Brisbane region in south east Queensland down the eastern mountainous areas and seaboard, south into Tasmania and west to at least the Grampian Mountains in Victoria. Three species of *Hadronyche* occur as isolates in southern Eyre Peninsula and the Lofty Ranges and southern Flinders Ranges in South Australia. The range of the two genera overlap. *Atrax* is more restricted and confined to the central part of the distribution of *Hadronyche* (see Fig. 1) e.g. from north of Sydney, west into the Blue Mountains, south across the border into Victoria and southwesterly into the highlands. An atracine has also recently been discovered in north Queensland (GRAY 1992). Although neither genus has been found in Western Australia there is the possibility that it may occur in confined areas in isolated southern areas of higher ground. If so it is likely to have a cryptozoic burrow like that of the South Australian species of *Hadronyche*.

Atrax robustus Cambridge, described in 1877, is abundant in central coastal New South Wales including suburban Sydney and it is this species which has earned world wide notoriety for funnel-webs due to its extreme toxicity to humans. Spiders excavate a shallow burrow or take advantage of crevices in logs or amongst stones from which extends a diffuse sheet-like web with two or several tubular entrances on the surface of the ground, against logs or amongst rocks. When closed the entrances collapse but open into funnel-like apertures when the spider is foraging.

In wet forest habitats the nests of *Hadronyche* range from similar sheet/funnel-webs in and on the ground, to tubular constructions extending from crevices on the trunks and branches of trees (MCKEOWN 1963; GRAY 1981, 1984*a*, 1992). In more sclerophyll habitats with dryer summers e.g. in South Australia, the nest may be a well-defined vertical burrow with a collar-like opening and a side-shaft closed by a vertically hinged door (MAIN 1964; GRAY 1984*b*).

The prey of both genera comprises predominantly invertebrates with a preponderance of arthropods, but as already stated vertebrates and particularly frogs are taken occasionally. Except for dispersing juveniles and reproductively active males, most mygalomorphs are more or less sedentary and adult females rarely move



FIGS 1–4

1: distribution of *Atrax* and *Hadronyche* (after GRAY 1988); 2–4: geographic ranges of three species of bandicoots, see text for discussion; 2 *Perameles nasuta*; 3: *Isoodon macrourus*; 4: *I. obesulus* (species now extinct in grey area of indicated geographic range). 2, 3, 4 after Stodart, Gordon and Braithwaite respectively (*in* STRAHAN 1983). The subspecies distribution boundaries for each of the bandicoot species not indicated.

far, if at all from their burrows. However, female funnel-webs, at least of *Atrax robustus* are apparently relatively mobile. GRAY (1981) attributed their movements to rain or other disturbances whereas BRADLEY (1993) collected vagrant females in pitfall traps at all seasons but with higher numbers after rain.

Venom and effects on humans. The venom contains a neurotoxin ("atraxotoxin") which acts on the nerve fibre membranes of susceptible organisms e.g. primates, at least rhesus monkeys and humans. It apparently elicits the release of acetylcholine in the autonomic nervous system (SUTHERLAND 1974). The debilitating symptoms include vomiting, muscle spasms, salivation, pulmonary oedema, coma and finally respiratory failure and cardiac arrest (SUTHERLAND 1974, 1976, 1978). SUTHERLAND (1978) summarised the chemistry of the venom as comprising several components, namely (and in the greatest proportion) gamma aminobutyric acid (GABA) which also occurs in other spider toxins, an indole lactic acid-spermine complex, hyaluronidase and the, at that time, chemically unidentified atraxotoxin. More recently, SHEUMACK *et al.* (1985) have isolated and analysed the lethal components of *Atrax robustus* toxin ("robustoxin") as a unique amino-acid sequence. BROWN *et al.* (1988) have demonstrated a similar structure ("versutoxin") in the venom of *Atrax versutus* (this species is now included in *Hadronyche* (GRAY 1988)).

In that it is during summer that anxiety about funnel-webs is most pronounced it is of interest that both male and female spiders produce more potent venom during this season than at other times of the year (ATKINSON 1981*b*), who also showed that repeated milking of spiders reduced the volume and potency of the venom. It may be that in the many cases of little response to bites by humans, the spiders have recently fed and spent much of their venom or that they simply have not released the venom.

Response of other vertebrates to toxicity. While humans and rhesus monkeys are paticularly vulnerable to the venom of the Sydney funnel-web (*Atrax robustus*) conversely many other vertebrates show indisposition of only short duration e.g. sheep and horses (WIENER 1963, cited in SUTHERLAND 1978) or no serious or lasting effects, notably rats, cats and rabbits, and some species are variably responsive to the venom e.g. mice and guinea pigs (WIENER 1957). The introduced toad *Bufo marinus* is also resistant to the venom (SUTHERLAND 1978). ATKINSON (1981a) demonstrated an inhibitory factor (*Atrax* venom inhibitor or A.V.I. of which the chemical identity is not known) in the plasma of those vertebrates which were not seriously affected by funnel-web venom. Furthermore he showed that mice, pigeons, cats, rats, pigs, rabbits and dogs, sheep, cattle, horses and cane toads had this component in various proportions.

ATKINSON (1981*b*) demonstrated that other species of funnel-web spiders for which toxicity has been tested e.g. *Hadronyche infensa*, *versuta* and *formidabilis* are equally as venomous as *Atrax robustus*.

Relevant to the thesis presented here is the evidence, both circumstantial and recorded, that indiginous bandicoots (in addition to those introduced animals mentioned above) are apparently immune to the funnel-web venom. Indeed it is surprising that experimental work has not been directed to bandicoots or other indiginous vertebrates.

Finally it is alleged that the toxic component which affects vertebrates (e.g. primates) is not the same component of the venom that kills the spider's "normal prey" (GRAY 1992) as also implied by SUTHERLAND (1978) when referring to the composition of funnel-web venom.

BANDICOOTS

Taxonomic Position and Palaeontological history. Australian "bandicoots" (Peramelidae) are marsupials which derive their common name from their general similarity in appearance and habit to the rat-like rodent bandicoots of the Indian region.

There is general acceptance that perameloids arose in Australia as one divergent group from early polyprotodont syndactylous marsupials, which had already separated (about 50 mya) from an ancestral australidelphian stock (STRAHAN 1990).

Perameloids including "ordinary and forest bandicoots" are present in early Eocene deposits at Tingamurra in southeast Queensland (ARCHER *et al.* 1994, p. 80) which area the authors infer had a uniformly mild to warm climate at that time. They also noted that the only mammals present appeared to be insectivorous and omnivorous marsupials. Extant genera including *Perameles* occur in Pliocene deposits at Bluff Downs in northeast Queensland (ARCHER & WADE 1976; ARCHER & HAND 1984, p. 542). Numerous sub-fossil deposits of extant species of Perameles and Isoodon are also known from South Australia (KEMPER 1990) and Western Australia (FRIEND 1990).

Geographic distribution and habitat. Four genera of the Peramelidae occur in Australia although one, *Chaeropus* is believed to have become extinct since European settlement. Both the common genera, short nosed and long nosed bandicoots, *Isoodon* and *Perameles* respectively enjoyed a wider geographic range at the time of European settlement than today. They include species which occur occasionally in rainforests, but more commonly from wet sclerophyll forests to woodland and arid habitats in favourable areas across the continent. Those of arid habitats have suffered greater geographic contraction. The three commonest species and which are of most relevance to this discussion are *Isoodon macrourus* (Fig. 3) with the most extensive range across northern Australia and down the east coast, *I. obesulus* (Fig. 4) and *Perameles nasuta* (Fig. 2). All three species have geographic subspecies. The range of *I. macrourus* and *P. nasuta* overlaps in mid eastern Australia and the distribution of the southern brown bandicoot (*I. obesulus*) and *P. nasuta* coincides in southeastern Australia. *I. obesulus* (Fig. 4) is the only one of the three species which occurs in southwestern Australia and southern South Australia (KEMPER 1990; FRIEND 1990). Other species of both genera occur in South Australia and northern Western Australia. Detailed accounts and maps of the current and historical distribution of extant species of both genera throughout the continent and Tasmania are given by various authors in SEEBECK *et al.* (1990).

Biology and prey. Bandicoots dig conical holes in litter and soil with their front claws and snouts while searching for prey or vegetable matter.

All bandicoots as well as eating plant material are carnivorous, feeding mainly on invertebrates such as earthworms and arthropods (DUFTY 1991) and occasionally small vertebrates such as frogs and lizards (HEINSOHN 1966). They also eat fungi (QUINN 1988; CLARIDGE *et al.* 1991). It is also noteworthy that the fearsome bull ant

(*Myrmecia*) is eaten. This would indicate that bandicoots could probably also cope with the perhaps no more formidable wandering male funnel-web spiders.

At least some species do indeed feed on spiders (GORDON 1983). QUINN (1988) noted in the faecal pellet analyses of *Isoodon obesulus* in southern Tasmania that amongst a wide range of invertebrate taxa, spiders were contained in 17 of the 48 scats analysed. CLARIDGE *et al.* (1991) also recorded spiders amongst faecal pellet analyses of *I. obesulus* and *P. nasuta* in southern New South Walses.

BOLAM (1930) records bandicoots of the Nullarbor region excavating and feeding on the "Trap-door spider", which from the quaint description was more likely to have been a door-building wolf spider (Lycosidae) than a mygalomorph. I have occasionally seen mygalomorph burrows disturbed by conical excavations which were attributed to bandicoots. R. Atkinson (pers. comm.) quotes a hear-say report of a local resident having found "twenty five funnel-web spiders" in the stomach of a road-killed bandicoot in the Wollongong area of New South Wales. GRAY (1987) refers to the cryptozoic nest entrances of some funnel-web species which thereby prevent detection by "predators such as bandicoots...". Finally WISHART (1992) infers a population increase of several species of mygalomorphs in a remnant patch of rainforest at Gerringong New South Wales to the decline of bandicoots which could previously have had a subduing effect on the spiders through predation.

DISCUSSION

Behavioural interaction of funnel-webs and bandicoots. Today the distribution of bandicoots of one or more species coincides with the range and actual occurrence of funnel-web spiders. There is no fossil history of funnel-webs but because they lack affinity with any known genera except possibly *Porrhothele* (GRAY 1988; RAVEN 1985) extreme antiquity can be argued. This assumption together with the fragmented range (between South Australia and the Grampian Mountains in Victoria (MAIN 1964, 1976, 1984, p. 73; GRAY 1987, 1988) and the Brisbane and Daintree areas in Queensland (GRAY 1992)) suggests a once continuous and possibly wider range than that of today. Bandicoots occur in the same general forest and low woodland habitats as funnel-webs and forage in patches of open ground and amongst low vegetation. Contact with the spiders while rootling and nosing in their shared habitats must frequently occur and has probably been continuous from amongst their antecedents of the early Tertiary (or earlier) to the present. As already discussed Perameloid fossil history goes back to at least early Eocene (ARCHER *et al.* 1994) which suggests the possibility of a long period of behavioural overlap with funnel-webs.

Possibly the bandicoots would early on have "tested" the spiders as prey, both juveniles and females disturbed in their nests and especially wandering males. As has been shown already, spiders comprise a substantial component of bandicoot diet (GORDON 1983; QUINN 1988; CLARIDGE *et al.* 1991). HEINSOHN (1966) remarked on the habit of both *Isoodon* and *Perameles* species "rolling" and kneading with their front feet, potential prey, particularly unfamiliar quarry. Such behaviour with a funnel-web may sometimes result in a bite. Thus spiders with relatively stronger toxin

(which initially would have been advantageous for subdueing larger or more than usually active invertebrates) could have been selectively favoured if giving a predatory bandicoot a nip on the nose. But over time bandicoots with some resistance would also have had a selective advantage. Incremental increase in toxicity of the spiders could have resulted in the current hypothesised situation with the bandicoot now one step ahead in the "arms race". Such a hypothesis is in accord with the Red Queen Hypothesis (VAN VALEN 1973, 1977, 1983) which in its broad interpretation implies that one or other species in a confrontation is never the all-out winner.

Isoodon obesulus, *I. macrourus*, *Perameles nasuta* all, in part, coincide with the present range of *Atrax* and *Hadronyche* — the latter two species of bandicoots with both genera of spiders and *I. obesulus* with *Hadronyche* in South Australia. In that *I. obesulus* also extends into Western Australia, where funnel-webs are unknown, in order to test the hypothesis proposed, the immunity of *Isoodon* from areas where funnel-webs are absent (as well as where present) needs to be tested. It is possible that outside the funnel-web spiders' range, bandicoots are not resistant to the venom.

The above hypothesis may explain the "evolution" of the venom and the countering response by bandicoots . However, it does not explain how it is that many other animals which have had no historical association with funnel-webs, are immune or at least contain in their blood a venom inhibiting chemical e.g. *Atrax* venom inhibitor or A.V.T. (ATKINSON 1981*a*).

Alternatively, if indeed bandicoots are immune then the inhibitor may be a more or less universal factor in the blood of most animals (with the exception of at least some primates) which now fortuitously protects them against envenomation by funnel-webs. Again I am surprised that no experimental work has been conducted on bandicoots or any other indiginous vertebrates! Presumably because medically oriented workers have been involved with trying to find an antidote rather than a cause.

Bandicoot resistance to "tick bite". It is perhaps pertinent that there is a further well hnown example of tolerance by bandicoots (and some other indiginous marsupials) to an arachnid toxin, that is to "tick bite".

The southern brown bandicoot, *Isoodon macrourus* (in the mid-eastern part of its range) habitually carries a high load of the paralysis tick *Ixodes holocyclus* without displaying discomfort as does also but perhaps to a lesser extent the long nosed bandicoot *Perameles nasuta* and like-wise several other indiginous mammals, birds and reptiles (DAUBE 1975). In contrast, the tick is highly toxic to domestic animals (KAIRE 1966) and humans (BANFIELD 1966; GILL 1966). One suggestion for the apparent immunity of bandicoots is that individual bandicoots develop an immunity over time as a result of successive infestations by tick larvae (R. Atkinson, pers. comm.). However it would be interesting to test the immunity of bandicoots from areas outside the range of *I. holocyclus*.

Anotable example of coevolutionary response to toxins in Australian biota. Relevant to the possibility of geographic variation in immunological response to

toxins is the case of tolerance to toxic plants of the genera *Oxylobium* and *Gastrolobium* by herbivorous marsupials in southwestern Western Australia. In contrast subspecific counterparts in eastern Australia, outside the range of these plants are susceptible to the toxin (monosodium fluororoacetate) (OLIVER *et al.* 1977). Such geographic variability in toxin tolerance suggests a co-evolutionary interaction akin to a predator/prey conflict and counter-ploy as suggested above for the bandicoot and funnel-web.

Examples of predator/prey coevolution where toxin is involved. Analogous to the above proposed current "success story" of a predator in conflict with a toxic prey (i.e. bandicoot a step ahead of the funnel-web) is the case of the garter snake *Thomnophis sirtalis* which preys on the toxic newt *Taricha granulosa* which has the neurotoxin tetrodotoxin in its skin (BRODIE & BRODIE 1990). These authors demonstrate a coevolutionary response in that varying degrees of resistance are exhibited by the snakes depending on whether or not they occur together with the newt. With this demonstration the authors (BRODIE & BRODIE 1990) enhance credibility of the arms race analogy that previously suffered from "a bias toward explaining adaptation by the prey" which suggested that predators may not respond to such antipredator adaptations.

CONCLUSION

In applying this strengthened coevolutionary principle to the funnel-web/bandicoot hypothesis it is suggested that the bandicoot has responded to a dangerous prey. Of course this needs to be tested as stated above. It must also be borne in mind that funnel-webs may possibly in earlier times have been defending themselves also against other insectivorous /carnivorous marsupials. The more ferocious dasyurids began to diversify in the late Miocene (ARCHER *et al.* 1994) and it is possible that they, or ancestral forms, preyed on funnel-webs. Certainly we must look, not only at the present fauna, but give due consideration to actual and hypothetical antecedents. Both the fossil record of marsupials (ARCHER & HAND 1984) and the present wide but fragmented distribution of funnel-webs (*Atrax* and *Hadronyche*) (GRAY 1987, 1988, 1992; MAIN 1964) suggest a much wider and more continuous geographic range for bandicoots (and dasyurids) *and* spiders.

Should the above hypothesis be shown to be without support then we must ask again why the funnel-web is so venomous, particularly since the venom component which is toxic to humans is apparently not the same chemical component which kills its prey.

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Advances in the study of the spider fauna of ex-USSR

Kirill G. MIKHAILOV
Zoological Museum of the Moscow State University, Herzen Street 6, K-9, Moscow, 103009 Russia.

Advances in the study of the spider fauna of ex-USSR. - An updated catalogue of spiders of ex-USSR is compared with some earlier calculations of 1989. Up-to-date, 2672 spider species belonging to 470 genera and 49 families are reported from the ex-USSR territories. The main increase in species number since 1989 is found consecutively in Linyphiidae, Salticidae, Dysderidae, Gnaphosidae, Thomisidae, Lycosidae, and Clubionidae. Spider faunas of the ex-Soviet republics as much as of main physiographical regions are viewed. Areas of the most abundant spider diversity are consequently Russian Plain (1001 species), Caucasus (748), montaneous Middle Asia (706), mountains of South Siberia (700), Urals (689), Middle Siberia (568), and continental Far East (506). A large percentage of Linyphiidae is found in boreal areas, whereas Salticidae is mostly abundant in southern montaneous and desert areas.

Key-words: spiders – the ex-USSR territories – the ex-Soviet republics – fauna – catalogue

The results presented here are deriving from the compilation of a spider catalogue of USSR. The project was started in 1981, first preliminary data have been calculated in 1989, but were published only in part (MIKHAILOV 1992). A updated revised check-list is prepared for publication in "*Arthropoda Selecta*", and will be included in the book "Spiders of the ex-USSR territories: short catalogue and bibliography" to appear in 1996.

Aim of this project is the compilation of literature data. The bibliographical index comprises ca. 1,000 citations since the 18th century till 1995. A card catalogue of regional data is complete, but publication of all materials (comparable in volume with P. Bonnet's "Bibliographia araneorum") remains impossible due to a lot of technical reasons.

On the basis of my research, three periods in Russian/Soviet arachnological studies can be established:

- 18th century – 1860s: data accumulation,
- 1870s – 1967: descriptive faunistics,
- 1968 – until now: descriptive taxonomic period.

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A fourth, analytical period is still under way.

The first period started with the so-called Academician expeditions for the study of Russian nature (1760s–1770s), but only a handful of spider species were found, and most of the identifications remain doubtful. Scarce indications of spiders are dispersed among voluminous naturalists' books.

Arachnological papers as such appeared later, in 1870s, the highest number of faunistical articles having been published in 1910s–1920s. The main result of the second period is Charitonov's bilingual German-Russian catalogue (CHARITONOV 1932, 1936).

The third period started with three identification books (AZHEGANOVA 1968; UTOCHKIN 1968; TYSHCHENKO 1971). In 1980s, the number of faunistical and taxonomical papers was increased crucially and resulted in a new journal, "*Arthropoda Selecta*" launched in 1992.

Main results of spider study in Russia and other ex-USSR territories given hereinafter are arranged by the ex-Soviet republics, and then by physiographical areas (Tables 1–4, Maps 1–2).

TABLE 1

Generic/species composition of spider families known from the ex-USSR territories in 1995 (comparative data of 1989 are given in brackets)

Family	Number of genera		*Number of species*	
Atypidae	1	(1)	4	(2)
Ctenizidae	2	(2)	3	(3)
Dipluridae	1	(1)	1	(1)
Nemesiidae	2	(3)	11	(10)
Filistatidae	4	(1)	7	(6)
Sicariidae	1	(1)	1	(1)
Scytodidae	2	(1)	5	(2)
Leptonetidae	1	(0)	1	(0)
Pholcidae	5	(5)	16	(15)
Segestriidae	1	(1)	4	(4)
Dysderidae	6	(4)	92	(51)
Oonopidae	2	(2)	3	(2)
Palpimanidae	1	(1)	3	(3)
Mimetidae	2	(2)	6	(6)
Eresidae	2	(2)	2	(2)
Oecobiidae	4	(5)	7	(8)
Hersiliidae	1	(1)	3	(3)
Uloboridae	4	(4)	6	(6)
Nesticidae	3	(3)	14	(10)
Theridiidae	17	(17)	124	(116)
Theridiosomatidae	1	(1)	2	(2)
Linyphiidae	211	(153)	864	(654)
Tetragnathidae	7	(8)	45	(30)
Araneidae	18	(12)	112	(114)
Lycosidae	18	(14)	234	(210)
Pisauridae	3	(3)	13	(12)
Agelenidae	7	(4)	47	(44)

Cybaeidae	1	(1)	7	(3)
Argyronetidae	1	(1)	1	(1)
Desidae	1	(1)	6	(3)
Hahniidae	5	(4)	16	(10)
Dictynidae	14	(8)	52	(49)
Amaurobiidae	3	(2)	11	(9)
Titanoecidae	2	(2)	14	(13)
Zoropsidae	1	(1)	1	(1)
Oxyoidae	1	(1)	7	(6)
Anyphaenidae	3	(2)	5	(5)
Liocranidae	7	(4)	25	(19)
Clubionidae	2	(3)	104	(83)
Corinnidae	3	(4)	4	(5)
Zodariidae	3	(3)	22	(23)
Cithaeronidae	1	(0)	1	(0)
Prodidomidae	1	(1)	1	(1)
Gnaphosidae	28	(23)	245	(206)
Zoridae	1	(1)	7	(6)
Heteropodidae	3	(3)	5	(5)
Philodromidae	6	(4)	70	(61)
Thomisidae	17	(17)	172	(146)
Salticidae	39	(38)	267	(211)
TOTALLY 49 families	470	(375)	2672	(2184)

TABLE 2.

Generic/species composition of main spider families at the ex-USSR territories (in %)

No	*Family*	*% of genera*	*% of species*
1	Linyphiidae	45.0	32.4
2	Salticidae	8.3	10.0
3	Gnaphosidae	5.8	9.1
4	Lycosidae	3.8	8.8
5	Thomisidae	3.6	6.4
6	Theridiidae	3.6	4.6
7	Araneidae	3.8	4.2
8	Clubionidae	0.4	3.9
9	Dysderidae	1.3	3.4
10	Philodromidae	1.3	2.6
11	Dictynidae	3.0	1.8
12	Agelenidae	1.5	1.8
13	Tetragnathidae	1.5	1.7

Up-to-date, 2672 spider species belonging to 470 genera and 49 families are reported from the ex-USSR territories (Table 1). Since the 1989 evaluation, the main increase of species composition is recorded in Linyphiidae (+210 species), then successively in Salticidae (+55), Dysderidae (+41), Gnaphosidae (+39), Thomisidae (+26), Lycosidae (+24), and Clubionidae (+21). Two families, Leptonetidae and Cithaeronidae, are found in the ex-USSR territories in 1990s. It is possible to estimate now the volume of the total ex-USSR spider fauna to 3400–3500 species. These data are surpassing considerably my own earlier evaluation to 2700–3000 species

(MIKHAILOV 1992) and very close to calculations of Chinese spider fauna (ca. 3500 species – Song Daxiang, pers. comm.).

Linyphiidae shows the highest diversity in species and genera in ex-USSR (Table 2). Such enlarged share of linyphiids can be explained by the boreal position of the majority of ex-USSR areas, where this family is extremely diverse.

Analysis of spider faunas of the ex-Soviet republics (Table 3) indicates that Russia has the highest diversity, followed by Ukraine, Kazakhstan, and Azerbaijan. Faunas of Lithuania (with a surprisingly small part of linyphiids), Moldavia, and especially Armenia (with a large percentage of linyphiids, displacements in lycosids etc.) are not sufficiently studied.

TABLE 3

Species composition of seven main spider families at the ex-Soviet republics (in %)

Republic	Li	Sa	Gn	Ly	To	Te	Ar	Total (Species/ Families)
Russia	38.5	8.7	8.1	8.9	5.8	5.4	4.5	1822/37
Estonia	40.0	6.5	6.9	9.3	4.8	7.3	5.7	505/25
Latvia	35.7	7.8	8.6	10.9	4.8	7.6	7.3	397/20
Lithuania	19.7	5.5	8.0	16.0	6.7	5.9	10.9	241/21
Byelorussia	36.7	6.4	6.2	9.7	5.6	7.7	7.4	393/26
Ukraine	27.6	8.7	9.3	9.1	5.7	7.6	5.9	816/37
Moldavia	19.4	7.3	6.9	10.7	11.1	7.3	7.6	289/29
Georgia	22.4	4.6	4.9	8.0	8.3	6.4	9.2	327/35
Azerbaijan	16.1	13.2	10.2	8.6	7.3	7.7	6.3	509/35
Armenia	31.4	7.6	8.5	3.4	9.3	2.5	6.8	118/19
Kazakhstan	18.6	15.6	14.0	9.5	9.5	4.4	6.6	621/31
Uzbekistan	8.9	11.4	12.2	10.0	11.1	6.4	8.2	281/33
Turkmenia	10.0	15.7	16.3	7.1	8.6	4.7	6.5	339/38
Kirghizia	28.6	16.5	8.7	4.0	8.4	4.3	9.2	347/29
Tadjikistan	9.7	16.7	8.9	10.8	10.0	6.3	6.3	269/33

Abbreviations: Li – Linyphiidae, Sa – Salticidae, Gn – Gnaphosidae, Ly – Lycosidae, To – Thomisidae, Te – Theridiidae, Ar – Araneidae.

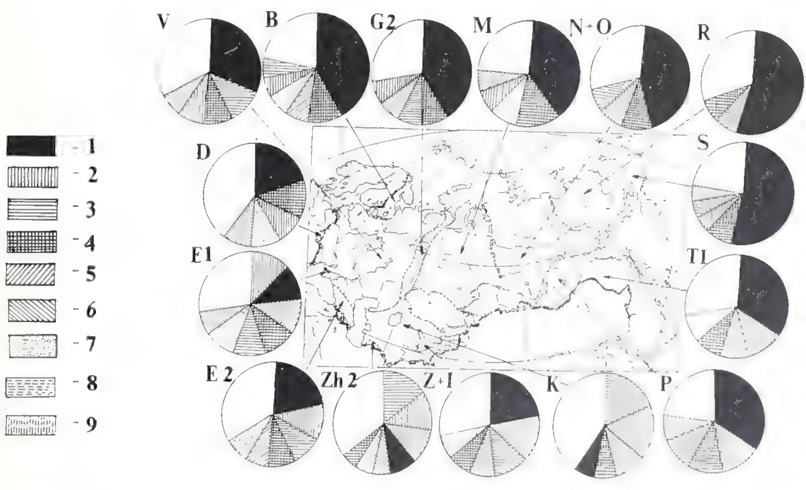
Among the 20 physiographical areas of ex-USSR established by GVOZDETSKY (1968) (Map 1), some are insufficiently explored (Zh1 – 126, L – 127 species), one possesses a poor fauna (G1 – 21 species) (Table 4). Areas of the most diverse spider faunas are successively the Russian Plain, the Caucasus (without Armenian upland), the montaneous Middle Asia, the mountains of South Siberia, Urals, Middle Siberia, and continental Far East. Main increase of species number during the last six years is recorded from the mountains of South Siberia (+264 species), the Far North-East, the W-Siberian Plain, and NE-Siberia (+195, +170, and +105 species, respectively).

Analysis of relative diversity of main spider families in physiographical area (Map 2) indicates the large part of linyphiids in boreal zone (B, G2, M, N + O, R, S), whereas Salticidae prefers southern montaneous and desert regions (Zh2, Z + I, K, P). High percentages of Clubionidae and Dysderidae in T1 and E2, respectively indicate certain centres of diversity of these families in those territories.

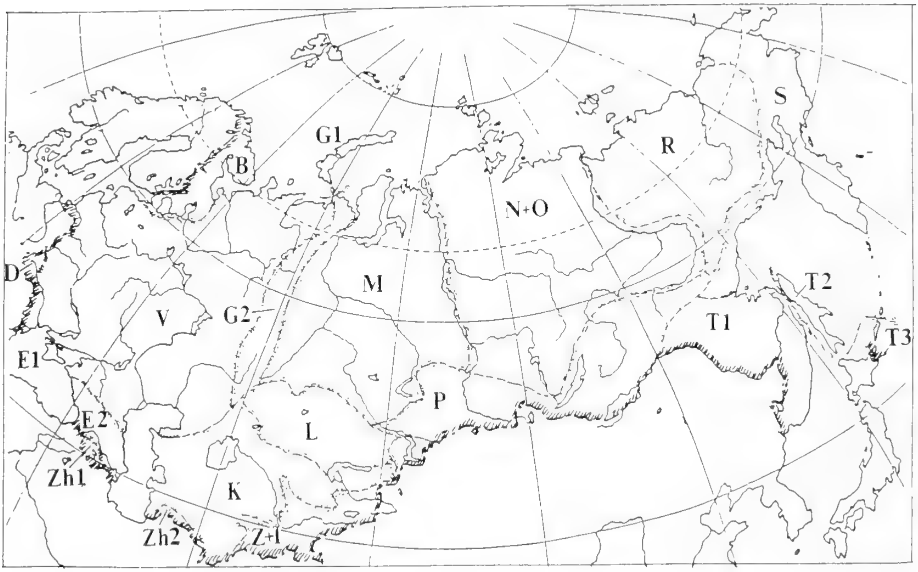
TABLE 4

Spider families/species composition in physiographical areas of ex-USSR in 1995 (comparative data of 1989 are given in brackets; areas are arranged after GVOZDETSKY 1968, with some changes)

Code	Area	Number of families	Number of species
B	Fennoscandia	25 (23)	423 (385)
V	Russian Plain	35 (36)	1001 (936)
G1	Novaya Zemlya	4	21
G2	Urals	24	689
G1 + G2		(25)	(600)
D	Carpathians	34 (35)	426 (435)
E1	Crimea	31 (31)	302 (308)
E2	Caucasus	40	748
Zh1	Armenian upland	19	126
E2 + Zh1		(40)	(671)
Zh2	Kopetdagh Mts.	37	214
Z + I	montaneous Middle Asia	38	706
Zh2 + Z + I		(42)	(650)
K	Middle Asian deserts	34 (37)	291 (291)
L	Kazakhstanian hills	18 (15)	127 (103)
M	W-Siberian Plain	21 (21)	413 (243)
N + O	Middle Siberia	22 (24)	568 (532)
P	mountains of S-Siberia	24 (23)	700 (436)
R	NE-Siberia	16 (16)	382 (277)
S	Far North-East	18 (16)	473 (278)
T1	continental Far East	24	506
T2	Saghalien	20	322
T3	S-Kuriles	18	142
T1 + T2 + T3		(25)	(375)



MAP 2. Contribution in species diversity of main spider families in some physiographical areas of ex-USSR. Abbreviations: 1 – Linyphiidae, 2 – Salticidae, 3 – Gnaphosidae, 4 – Lycosidae, 5 – Thomisidae, 6 – Theridiidae, 7 – Araneidae, 8 – Clubionidae, 9 – Dysderidae, others as in Map 1.



MAP 1

Physiographical areas of the ex-USSR territories (after GVOZDETSKY 1968, changed). Abbreviations: B – Fennoscandia, D. – Carpathians, E1 – Crimea, E2 – Caucasus, G1 – Novaya Zemlya, G2 – Urals, K – Middle Asian deserts, L – Kazakhstanian hills, M – W-Siberian Plain, N + O – Middle Siberia, P – mountains of South Siberia, R – NE-Siberia, S – Far North-East, T1 – continental Far East, T2 – Saghalien, T3 – S-Kuriles, V – Russian Plain, Zh1 – Armenian upland, Zh2 – Kopetdagh Mts., Z + I – montaneous Middle Asia.

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REVUE SUISSE DE ZOOLOGIE, vol. hors série: 479-489; août 1996

Vorläufige Beobachtungen zur Tag- und Nacht-Bewegungsaktivität der epigäischen Weberknechte (Opiliones, Arachnida) aus verschiedenartigen Habitaten im Vitoscha-Gebirge (Nordteil), SW-Bulgarien

Plamen MITOV
Department of Zoology and Anthropology, Faculty of Biology, University of Sofia, 8 Dragan Zankov Blvd., 1421 Sofia, Bulgaria.

Preliminary observations on diurnal locomotory activity of the epigeic harvestmen (Opiliones, Arachnida) in contrasted habitats of Vitosha Mountain (Northern part), SW Bulgaria. - In the present work the data from the investigations of the diurnal locomotory activity of 8 species Opiliones in the area of Vitosha Mt. are analysed. The material was collected with pitfall traps, situated near a river, in a forest and on a meadow, with a collecting period of 4 hours. Following these data, the species *Phalangium opilio* L., 1758, *Lophopilio palpinalis* (Herbst, 1799), *Opilio ruzickai* Šilhavý, 1938 are active by day and night, and the species *Paranemastoma radewi* (Roewer, 1926), *Rilaena balcanica* Šilhavý, 1965, *Lacinius horridus* (Panzer, 1794), *Lacinius dentiger* (C.L. Koch, 1848) and *Zacheus crista* (Brullé, 1832) are recognized as nocturnal.

Key-words: harvestmen - Opiliones - diurnal locomotory activity - Bulgaria

EINLEITUNG

Die Tag- und Nacht-Bewegungsaktivität der Weberknechte ist unzureichend erforscht. Angaben darüber gibt es in den Werken von PICKARD-CAMBRIDGE (1890), STIPPERGER (1928), KAESTNER (1931), TODD (1949), PABST (1953), IMMEL (1954), PFEIFER (1956), ŠILHAVY (1956), WILLIAMS (1962), PHILLIPSON (1960), EDGAR & YUAN (1968), STARĘGA (1976*a*, *b*), MARTENS (1978), CLOUDSLEY-THOMPSON (1978), HILLYARD & SANKEY (1989), MITOV (1993). Nur STARĘGA (1976*b*) gibt fragmentarische Daten aus Bulgarien zum Thema an. Der vorliegende Artikel presentiert die ersten speziellen Forschungen in dieser Hinsicht in Bulgarien.

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UNTERSUCHUNGSGELÄNDE

Die Untersuchung ist im Nordteil Vitoschas auf ca. 900 m ü NN (über Dragalevzi) in unmittelbarer Nähe des Flußes Dragalevska-Reka durchgeführt worden. Das Untersuchungsgelände besteht aus drei Habitatstypen: Wald (s. Abb. 1 A), Wiese (s. Abb. 1 B), und Flußuferzone (s. Abb. 1 C, D). Die Waldvegetation setzt sich aus Ass. *Carpinus betulus* + *Fagus sylvatica* - *Poa nemoralis* + *Galium odoratum*, die Wiesenvegetation - aus Ass. *Deschampsia caespitosa* + *D. flexuosa* + *Urtica dioica* - *Rubus idaeus* zusammen. Die Vegetation der Flußuferzone, die von Ass. *Carpinus betulus* + *Fagus sylvatica* - *Rubus idaeus* - *Carex* sp. geprägt ist, ist fast identisch mit der des

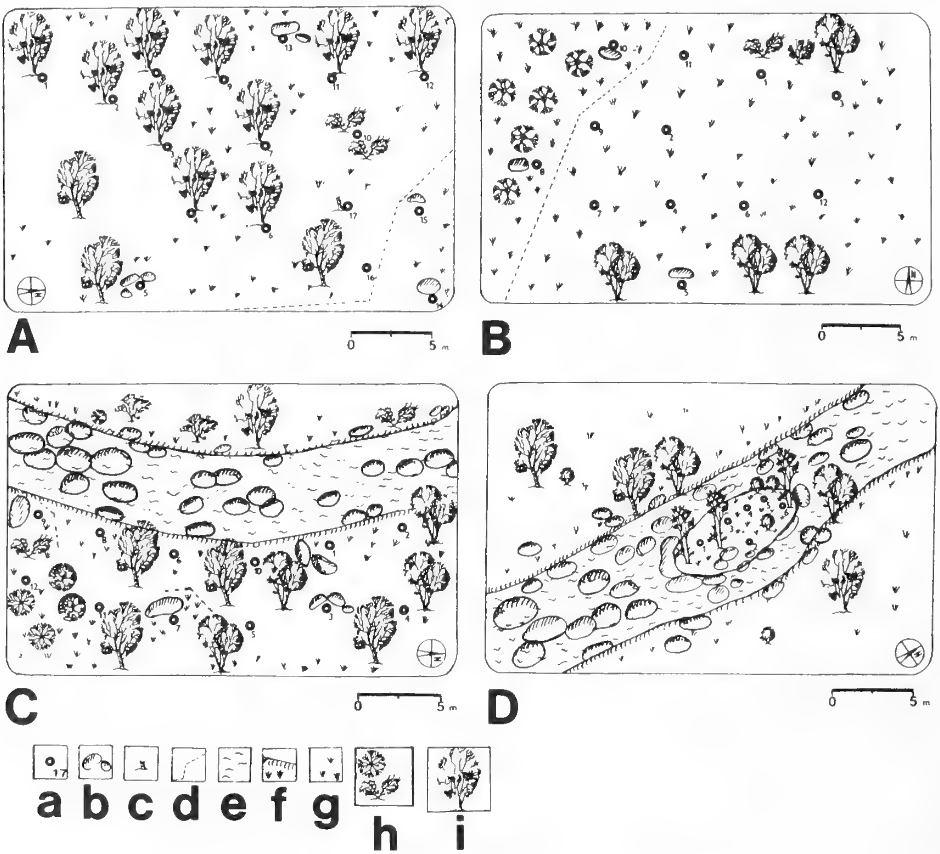

Abb. 1

Schema des Fallenansetzens in den erforschten Habitaten: A). Wald, B). Wiese, C). Uferzonen, D). Inselchen: a). Bodenfallen-Nr., b). Gesteine, c). verfaultes Wurzelwerk, d). Feuchtgegend, e). Fluß f). Uferstrich g).Graswuchs, h). Gebüsche, i). Bäume. Maßstab betrifft nicht die Baumhöhe.

Dauerinselchen des Flußes. Die untersuchten Habitate liegen sehr nah beieinander und sind leicht zugänglich. Die Bodenfallen blieben in denselben Habitaten über zwei Jahren in denselben Positionen und derselben Anzahl, die Aufsammlungen zeigten eine relativ große Vielfalt der lokalen Weberknechtfauna.

MATERIAL UND METHODEN

Die Untersuchung wurde mittels 47 Bodenfallen (Kunststoffbecher 500 ml, Höhe: 12 cm, Öffnungsdurchmesser: 9 cm, gefüllt mit Formalin (4 %), in der Wintersaison zusäzlich mit Äthylenglykol, ohne Schutzdach und Köder), in Abständen von 5 m (auf dem "Inselchen" 1,5-2,5 m) positioniert, durchgeführt. Nach Balogh (1958), hat Formaldehyd keine abstoßende oder anziehende Wirkung auf die Gliederfüßler. Adis (1979) hingegen gibt für Äthylenglykol und die Formaldehyd-lösungen (3-5%) vorwiegend einen anziehenden Wirkungseffekt an. Trotzdem bietet diese Methode zuverläßiger Ergebnisse im Vergleich zu dem periodischen Durchsuchen eines bestimmten Geländes (Todd 1949), da mit Bodenfallen die natürliche Bewegungsaktivität von Opiliones registriert wird.

Die Fallen wurden im Wald und auf der Wiese an mögliche Zufluchtsorte, die Weberknechte benutzen, gestellt. Da die Feuchtigkeit ein wichtiger Faktor ist, der die Aktivität der Weberknechte bestimmt (Todd 1949), wurden Fallen auch am rechten Ufer des Flußes Dragalevska-Reka (6 Fallen, 5 m vom Wasser entfernt, Durchschnittsfeuchtigkeit 70-80 % und 6 Fallen, 1 m vom Wasser entfernt, Durchschnittsfeuchtigkeit 100 %, Temperatur um 1° C niedriger s. Abb. 1 C) und auf einer Dauerinsel (Fläche: 15-20 m^2, s. Abb. 1 D) dieses Flußes aufgestellt.

Die Fallen wurden mit aufgehängten weißen Streifen markiert. Außer der Lufttemperatur wurde auch die Luftfeuchtigkeit mit einem Absorbtionshaarhygrometer in Bodennähe (2 cm) und in 2 m Höhe in allen Untersuchungsgebieten an derselben Stelle alle vier Stunden gemessen. Abb. 2 (a - e) zeigt eine Zusammenfassung der durchschnittlichen Messwerte. Die Untersuchungen wurden 1987 am 20.-21.05., 22.-23.08., 20.-21.11., und 1988 am 23.-24.02., 24.-25.05., 03.-04.09 durchgeführt. Eine Untersuchungsserie (23.-24.02.1988) verlief ohne Fang. Die Angaben zur Phänologie der Weberknechtarten, beruhen auf Aufsammlungen, die während 26 Monaten in 653 Fallen an 21 Punkten (800 m bis 2290 m) im Vitoscha-Gebirge getätigt worden sind.

ERGEBNISSE UND DISKUSSION

Bei der vorliegenden Analyse der 24-stündigen Bewegungsaktivität wurden berücksichtigt: Klimaverhältnisse, Belichtung, Angaben über die Ökologie, die Phänologie, Temperaturpräferenz und physiologischer Zustand (Hunger, Vermehrungsperiode u.a.) der Arten.

In den Fallen wurden 8 der insgesamt 17 im Untersuchungsgebiet nachgewiesenen Arten gefunden:

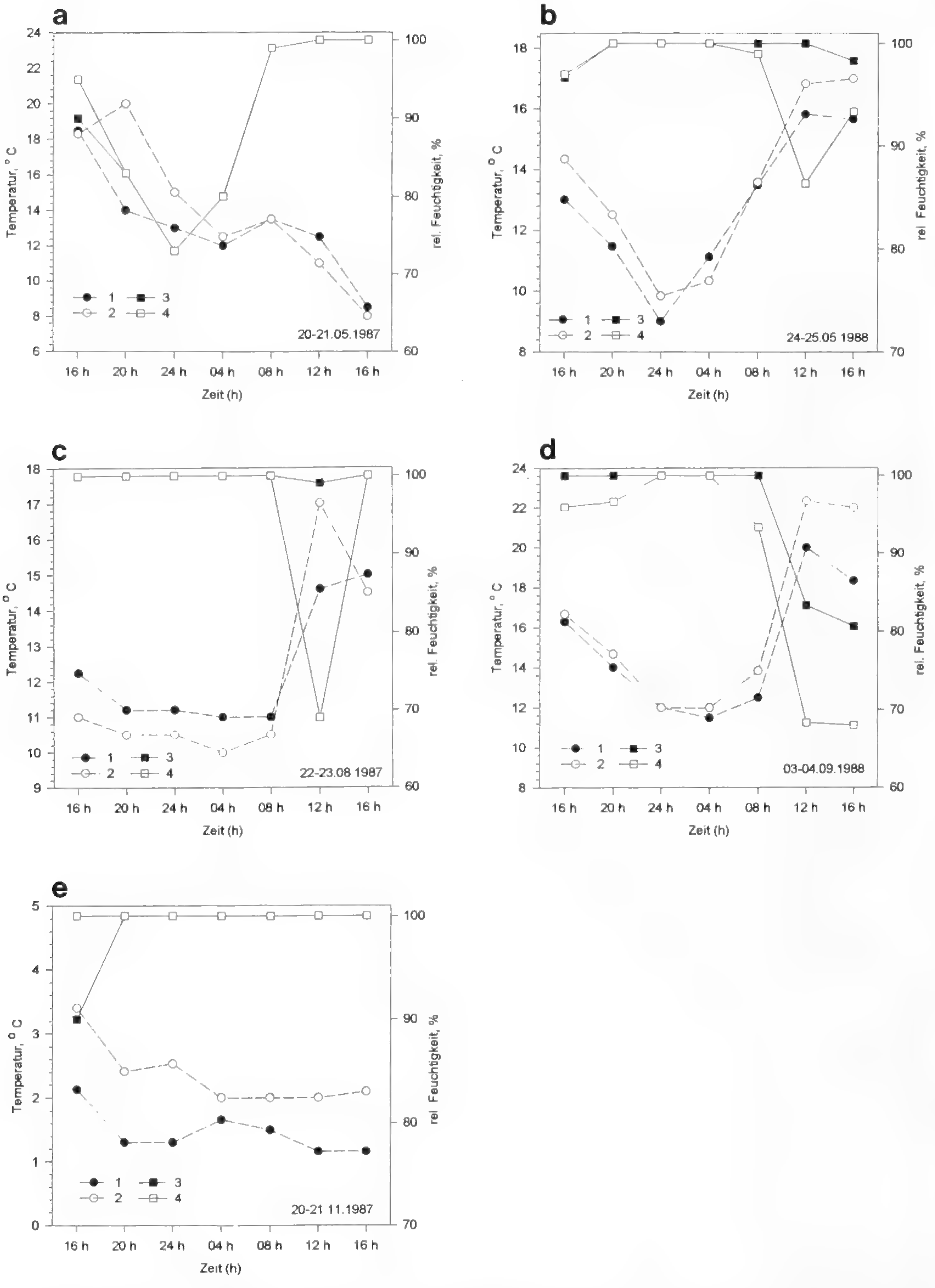

Abb. 2

Vertikalprofil der Durchschnittswerte der Lufttemperatur und der relativen Luftfeuchtigkeit auf dem Forschungsgelände von: a) 20.-21.05.1987, b) 24.-25.05.1988, c) 22.-23.08.1987, d) 03.-04.09.1988, e) 20.-21.11.1987. Lufttemperatur in Bodennähe (1) und in Höhe von 2 m (2); Relative Luftfeuchtigkeit in Bodennähe (3) und in Höhe von 2 m (4).

Paranemastoma radewi (Roewer, 1926) bewohnt schattige Orte, mit niedrigen Temperaturen und wo die Feuchtigkeit nahezu 100 % beträgt (STAREGA 1976*b*; MITOV 1986*b*). *P. radewi* hat eine schwache Toleranz gegen Trockenheit - sie stirbt innerhalb 25 Minuten bei Feuchtigkeit von 70 % und Lufttemperatur von 21° C, ihre Eier legt sie nur an sehr feuchte Orte ab (z.B. unter Gestein oder verfaulte Baumstrünke, in der Nähe von fließendem Wasser). Diese Art ist sehr häufig in den Höhlen Bulgariens (BERON 1994; BERON & MITOV, in press), die eine Durchschnittstemperatur 12° C und eine konstante, hohe Luftfeuchtigkeit besitzten. Das alles kann die Bewegungsaktivität dieser Art in der Nacht erklären. *P. radewi* ist vorwiegend in der Nacht in der Zeitspanne 20 h - 04 h aktiv (Tab. 1) und selten in der Zeitspanne 04 h-12 h und gerät in die Fallen, die sich in Zonen mit hoher Feuchtigkeit (95-100%) und

TABELLE 1

Tag- und Nacht-Bewegungsaktivität von *Paranemastoma radewi* Roewer aus Vitoscha-Gebirge. Abkürzungen und Zeichen: ●-Sonnenuntergang, ○-Sonnenaufgang, N - Bodenfallen-Nr., F - Fluß, Is - Inselchen

Datum:	Forschungszeitspannen (h)						Individuenzahl		
	16-20	20-24	24-04	04-08	08-12	12-16	mnl.	wbl.	juv.
		● 20 h 47'		☼ 05 h 59'					
20-21.V.1987			$N\ 4_{Is}$				_	2	_
		● 20 h 51'		☼ 05 h 56'					
24-25.V.1988		$N\ 8_F$ $N\ 1_{Is}$ $N\ 5_{Is}$	$N\ 1_{Is}$ $N\ 4_{Is}$	$N\ 1_{Is}$			8	6	1
		● 20 h 18'		☼ 06 h 42'					
22-23.VIII.1987		$N\ 5_{Is}$	$N\ 2_{Is}$		$N\ 8_F$		1	2	.
	● 19 h 57'			☼ 06 h 55'					
03-04.IX.1988			$N\ 1_{Is}$ $N\ 4_{Is}$				1	2	_

mit den niedrigsten Temperaturen (durchschnittlich 11,3° C) (s. Abb. 2 a-d) befinden, namentlich auf dem "Inselchen" und an dem Ein-meter breiten Uferbereich des Flußes (s. Abb. 1 C, D). Am 24.-25.05.1988 (s. Tab. 1) wurde eine höhere Aktivität zwischen 20 h und 08 h festgestellt, was mit der niedrigeren Temperatur und der höheren Feuchtigkeit in dieser Zeitspanne, im Vergleich mit derselben Zeitspanne vom 20.-21.05.1987 (s. Tab. 1; Abb. 2 A, B) erklärt werden könnte. Die relativ größe Anzahl aktiver Weibchen weist möglicherweise, auf einen Zusammenhang mit der Eierablage hin (Ende Mai treten Weibchen mit entwickelten Eiern auf und Anfang Juni sind Gruppen gelegte Eier zu finden). Die Bewegungsaktivität von *P. radewi* ist am 22.-23.08.1987 sehr hoch und wird sogar in die Tageszeit (08 h - 12 h) verlegt (s. Tab. 1). Das ist vielleicht auf den am 22.08. gefallenen Regen und das kalte und

TABELLE 2

Tag- und Nacht-Bewegungsaktivität von *Rilaena balcanica* Šilhavý aus Vitoscha-Gebirge. Abkürzungen und Zeichen: ●-Sonnenuntergang, ○-Sonnenaufgang, N - Bodenfallen-Nr., Wd - Wald, F - Fluß.

Datum:	Forschungszeitspannen (h)						Individuenzahl		
	16-20	20-24	24-04	04-08	08-12	12-16	mnl.	wbl.	juv.
		● 20 h 47'		○ 05 h 59'					
20-21.V.1987		N 5_{Wd} N 10_{Wd}	N 5_F N 11_F N 13_{Wd}				2	3	_
		● 20 h 51'		○ 05 h 56'					
24-25.V.1988	N 11_F	N 6_F N 9_F N 12_F	N 4_{Wd}	N 5_{Wd}			4	6	_
		● 20 h 18'		○ 06 h 42'					
22-23.VIII.1987		N 6_F					3	_	_
	● 19 h 57'			○ 06 h 55'					
03-04.IX.1988	N 6_F	N 2_{Wd} N 8_{Wd}	N 14_{Wd}				_	_	4
	● 17 h 00'			○ 06 h 42'					
20-21.XI.1987			N 11_F				_	_	1

wolkige Wetter zurückzuführen, da geringere Sonnenscheine, niedrigere Temperaturen und hohe Luftfeuchtigkeit diese Art zu erhöhter Aktivität stimulieren. Auch könnte diese Aktivitätsverlegung in den Tag (08 h - 12 h) auf Hunger zurückzuführen sein. Nach WILLIAMS (1962) verlegt sich die Aktivität des Tieres in frühere Stunden, wenn eine Nahrungsaufnahme wegen ungünstiger Klimaverhältnisse nicht möglich war. Die zwischen 24 h - 04 h am 03.-04.09.1988 beobachtete Aktivität unterstreicht die Bedeutung niedriger Temperaturen und hoher Luftfeuchtigkeit auf die Bewegungsaktivität. Die im November fehlende Aktivität entspricht den phänologischen Angaben - in diesem Monat ist *P. radewi* sehr selten zu finden.

Rilaena balcanica Šilhavý, 1965 ist eine Art, die bevorzuglich schattige, feuchte und kühle Orte besiedelt (MITOV 1986*a*). In Bulgarien wurde sie vor allem in Laubwäldern gefunden, wo sie sich im Fallaub versteckt (STARĘGA 1976*b*; MITOV 1986*a*). Daher befinden sich alle Fallen, in die *R. balcanica* geraten ist, in der Nähe von Steinen und einer dicken Fallaubschicht (s. Abb. 1 A, C). Eine Aktivität konnte hauptsächlich in der Nacht (20 h - 04 h) festgestellt werden (s. Tab. 2), sie war bei niedrigerer Lufttemperatur und höherer Luftfeuchtigkeit am 24.-25.05.1988 größer als am 20.-21.05.1987 (s. Abb. 2 a, b). Die Nachtaktivität dieser Art ließ sich auch im Laborversuch (s. MITOV, 1988) nachweisen. Ende Mai und im Juni sind zahlreiche geschlechtsreife Tiere zu finden. Die erhöhte Zahl der Jungtiere und deren hohe

Aktivität Ende August und Anfang September spiegelt sich im den Fallenfängen am 03.-04.09.1988 wider. Im November nimmt die Zahl der Jungtiere deutlich ab.

Lacinius horridus (Panzer, 1794). Nach Angaben von PFEIFER (1956), ŠILHAVY (1956) und STARĘGAS (1976*a*) ist diese xerophile Art tagaktiv. Unsere Ergebnisse (Tab. 3) bestätigen STARĘGAS (1976*b*) Behauptung, über dessen Nachtaktivität. Während der Frühjahrsuntersuchung wurden keine Adulti gefunden, Jungtiere treten erst später (Juni) auf. Wahrscheinlich ist die schwache Aktivität während der späteren Untersuchungen (22.-23.08.1987, 03.-04.09.1988 und 20.-21.11.1987) auf die niedrigen Temperaturen zurückzuführen.

TABELLE 3

Tag- und Nacht-Bewegungsaktivität von *Lacinius horridus* Panzer aus Vitoscha-Gebirge. Abkürzungen und Zeichen: ●-Sonnenuntergang, ☼-Sonnenaufgang, N - Bodenfallen-Nr., Wd - Wald, Is - Inselchen.

Datum:	Forschungszeitspannen (h)						Individuenzahl		
	16-20	20-24	24-04	04-08	08-12	12-16	mnl	wbl.	juv
		● 20 h 18'		☼ 06 h 42'					
22-23.VIII.1987		N 5_{Wd}					–	1	–
	● 19 h 57'			☼ 06 h 55'					
03-04.IX.1988		N 6_{Is}					–	1	
	● 17 h 00'			☼ 06 h 42'					
20-21.XI.1987			N 10_{Wd}				1	–	.

Lophopilio palpinalis (Herbst, 1799) (s. Tab. 4) ist eine (hemi-) hygrophile Waldform, die in den oberen Bodenschichten, an feuchten Orten (MARTENS 1978) zu finden ist. TODD (1944), PFEIFER (1956), WILLIAMS (1962), STARĘGA (1976*b*), und HILLYARD & SANKEY (1989) erwähnen seine Nachtaktivität.

Die Verbreitung dieser Art, und ihre Phänologie weisen auf eine Bevorzugung niedriger Temperaturen hin. Im Vitoscha-Gebirge ist *L. palpinalis* schon Anfang Januar aktiv, Weibchen mit entwickelten Eiern und Männchen sind zu finden. Adulti waren nur in geringer Zahl in der Fallen tags und nachts vom 20.-21.05.1987 und vom 24.-25.05.1988 enthalten. Nachtaktivität von Jungtieren konnte während der Nacht vom 20.-21.05.1987 im Wald neben der Falle Nr. 17 auf kurzen Strecken beobachtet werden. Die ersten, wenigen Jungtiere sind auf 900 m ab Anfang Mai bis Juli und August anzutreffen. Der Regen am 22.-23.08.1987, die hohe Bewölkung, die Temperaturerniedrigung unter 12° C und die beinahe 100%-ige Feuchtigkeit (s. Abb. 2 c) haben wahrscheinlich die zu dieser Zeit selten zu findende Adulti in die auf den feuchtesten Orten plazierten Fallen (s. Tab. 4) geführt. Tiere diser Art scheinen

TABELLE 4

Tag- und Nacht-Bewegungsaktivität von *Lophopilio palpinalis* (Herbst) aus Vitoscha-Gebirge. Abkürzungen und Zeichen: ●-Sonnenuntergang, ○-Sonnenaufgang, N - Bodenfallen-Nr., Wd - Wald, F - Fluß, Is - Inselchen.

Datum:	Forschungszeitspannen (h)						Individuenzahl		
	16-20	20-24	24-04	04-08	08-12	12-16	mnl.	wbl.	juv.
	● 20 h 18'			○ 06 h 42'					
22-23.VIII.1987	N 2_{Is}	N 2_{Is} N 3_{Is}					–	4	–
	● 19 h 57'			○ 06 h 55'					
03-04.IX.1988	N 3_{Is}	N 1_{F}	N 6_{Is}					2	1
	● 17 h 00'			○ 06 h 42'					
20-21.XI.1987	N 15_{Wd} N 16_{Wd}		N 16_{Wd} N 1_{Is}	N 14_{Wd}	N 17_{Wd} N 3_{Is}		5	3	–

sowohl am Tag (16 h- 20 h) als auch in der Nacht (20 h - 24 h) aktiv zu sein. Anfang September treten nochmals Jungtiere auf und Mitte und Ende dieses Monates Weibchen ohne entwickelte Eier und Männchen, was in Verbindung mit dem wolkigen und windigen Wetter, die Zahl der am 03.-04.09.1988 erbeuteten Individuen (s. Tab. 4) beeinflußt zu haben scheint. Die Bewegungsaktivität von *L. palpinalis* äußert sich wieder am Tage (16 h - 20 h), jedoch mit einer verlängerten Zeitspanne in der Nacht (von 20 h bis 04 h). Am 20.-21.11.1987, unabhängig von den niedrigen Lufttemperaturen der oberen Bodenschicht (durchschnittlich 1,46° C) (s. Abb. 2 e), wurde eine gleichbleibende Bewegungsaktivität von 16 h bis 12 h (s. Tab. 4) beobachtet. Diese erhöhte Aktivität und die größere Anzahl gefangene Männchen und Weibchen, hängt vielleicht mit der Vermehrungsperiode (MARTENS 1978) zusammen, was auch eigene Beobachtungen bestätigen. Wahrscheinlich suchen die Weibchen nach der Kopulation feuchtere Orte auf um die Eier abzulegen, weshalb vielleicht *L. palpinalis* nur in die an feuchten Orten im Wald und auf dem "Inselchen" (s. Abb. 1 A, D; Tab. 4) plazierten Fallen gerät. *L. palpinalis* scheint vorwiegend nachtaktiv zu sein; diurne Aktivität könnte durch günstige Klimaverhältnisse verursacht sein oder im Zusammenhang mit der Vermehrung zu stehen.

Opilio ruzickai Šilhavý, 1938 bewohnt waldige, mäßig feuchte und sehr schattige Habitate. Sie ist nachtaktiv (STARĘGA 1976*b*, MARTENS 1978). Eine Bewegungsaktivität von vorwiegend juvenilen bodenbewohnenden Tieren (MARTENS 1978) wurde nur im Mai fesgestellt. Bevorzugt waren Fallen im Bereich der Fallaubanhäufungen von Steinen und anderen feuchten Orten (s. Abb. 1 A, C, D; Tab. 5). Der geringere Fang von Adulten erklärt sich durch deren arboricole Lebensweise (MARTENS 1978). Im August, Anfang September, und November ist *O. ruzickai* verhältnismäßig selten zu treffen.

Lacinius dentiger (C.L. Koch, 1848), ist nach Staręga (1976*b*) und Martens (1978) nachtaktiv. Am 25.05.1988 wurden am Fuß der Baumstämme immobile Jungtiere am Tag (08 h -12 h) beobachtet. Am 03.-04.09.1988 um 21 Uhr wurden 2 Weibchen im Wald auf der Blättermasse zwischen den Fallen Nr. 8 und Nr. 9 und am 04.09. am Tag (09) Uhr 1 Männchen an einem Baumstamm gefunden (siehe auch Martens 1978), was die geringe Zahl der gefangenen Adulten in dieser Zeitspanne erklärt. Außerdem sind Adulti von August bis November seltener.

Zacheus crista (Brullé, 1832): Die Aktivität dieser Art am 24.-25.05.1988 und andere eigene Beobachtungen bestätigen die Literaturhinweise (Staręga 1976*b*), daß diese Art nachtaktiv ist (s. Tab. 5). Im Vitoscha-Gebirge (800-900 m) nimmt die Individuenzahl dieser Art in den Monaten August - Oktober deutlich ab, November und Dezember ist sie nicht zu finden. Die Juvenilen erscheinen Anfang April und sind zahlreich im Mai-Juni. Es ist eine thermophile Art (Martens 1978) und es ist möglich, daß der Regen und die niedrigen Temperaturen am 22.-23.08.1987, das

Tabelle 5

Tag- und Nacht-Bewegungsaktivität von *Opilio ruzickai* Šilhavý *Lacinius dentiger* (C.L. Koch), *Zacheus crista* (Brullé) und *Phalangium opilio* L. aus Vitoscha - Gebirge. Abkürzungen und Zeichen: ●-Sonnenuntergang, ○-Sonnenaufgang, N - Bodenfallen-Nr., Wd - Wald, We - Wiese, F - Fluß, Is - Inselchen.

Arten	Forschungszeitspannen (h)						Individuenzahl		
Datum:	16-20	20-24	24-04	04-08	08-12	12-16	mnl.	wbl.	juv.
Opilio ruzickai		● 20 h 47'		○ 05 h 59'					
20-21.V.1987	N 1$_{Wd}$	N 6$_{Wd}$ N 7$_{Wd}$			N 10$_{Wd}$		–		4
		● 20 h 51'		○ 05 h 56'					
24-25.V.1988	N 3$_{F}$	N 7$_{Wd}$ N 9$_{Wd}$ N 1$_{Wd}$ N 4$_{Is}$					1	–	4
Lacinius dentiger		● 20 h 51'		○ 05 h 56'					
24-25.V.1988		N 8$_{F}$					–		1
Zacheus crista		● 20 h 51'		○ 05 h 56'					
24-25.V.1988		N 3$_{We}$ N 7$_{We}$					–	–	2
Phalangium opilio		● 20 h 18'		○ 06 h 42'					
22-23.VIII.1987		N 9$_{We}$					–	1	
	● 19 h 57'			○ 06 h 55'					
03-04.IX.1988	N 2$_{We}$				N 2$_{We}$ N 7$_{We}$	N 8$_{We}$	2	5	

windige und wolkige Wetter am 03.-04.09.1988, sowie die oben erwähnten phänologischen Eigentümlichkeiten den Fang während des gesamten Untersuchungszeitraums stark beeinflußt haben.

Phalangium opilio Linnaeus, 1758. PFEIFER (1956) und MARTENS (1978) erwähnen diese Art als tagaktiv. Andere Autoren (ŠILHAVY 1956; STARĘGA 1976*a*, *b*; EDGAR & YUAN 1968) melden *Ph. opilio* als vorwiegend nachtaktiv, aber auch als tagaktiv. Sie war am 22.-23.08.1987 in der Nacht aktiv (Tab. 5). Vielleicht hat der Regen am 22.08. die Aktivität von *Ph. opilio* am Tag in die Zeitspanne von 20 h - 24 h verlegt, weil die betroffenen Tiere hungrig waren (s. WILLIAMS 1962). Eine diurne Bewegungsaktivität wurde am 03.-04.09.1988 in der Zeitspanne von 16 h - 20 h und von 08 h - 16 h beobachtet, als die Temperaturen am höchsten waren (s. Abb. 2 d). Die beobachtete Aktivität könnte im Zusammenhang mit der Temperaturpräferenz (zwischen 13,4° C und 17,6° C Mittelwert: 15,5°C, (TODD 1949)) dieser Art stehen, da die durchschnittliche Lufttemperaturen in der oberen Bodenschicht der Wiese zwischen 16 h - 20 h, 20 h - 08 h und 08 h - 16 h 14.5° C, 11,1° C 15°C betrugen. Futtererwerb von *Ph. opilio* (MITOV 1988) und Kopulation am Tage konnte im Vitoscha-Gebirge, beobachtet werden. *Ph. opilio* ist im Mai und November auf 800-900 m sehr selten anzutreffen.

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Dynamics of a population of burrowing wolf spiders. Is there any competition?

Jordi MOYA-LARAÑO, Juan Manuel ORTA-OCAÑA,
José Antonio BARRIENTOS & Antoni CASES
Unitat de Zoologia. Departament de Biologia Animal, Biologia Vegetal i Ecologia. Universitat Autònoma de Barcelona. E-08193 Bellaterra (Barcelona), Spain.

Dynamics of a population of burrowing wolf spiders. Is there any competition? - Population dynamics of the wolf spider *Lycosa tarentula fasciiventris* (Dufour, 1835) (Araneae, Lycosidae) has been studied for almost a complete year. The distribution patterns of the burrows and the developmental stage, sex, prosoma and patella-tibia length of the burrow occupants were collected fortnightly during that period. Individuals were marked after each moult. *L. tarentula* seems to be a biannual and iteroparous species. There were peaks in burrow recruitment of the one-year-old juveniles in September (after the spiderlings hatched) and in August (after the adult males leave their burrows searching for mates). These recruitment periods can be explained by a lack of competition. The juveniles, after occupying a burrow, can either stay inside until adulthood or leave it. We present a preliminary Cox proportional hazards regression model, showing a pattern of density-dependent burrow leaving for juveniles. Interference competition for burrow-sites could play a role in population regulation.

Key-words: *Lycosa tarentula fasciiventris* - burrowing wolf spiders - population dynamics - Thiessen polygons - interference competition - burrow-site

INTRODUCTION

The role of competition for food resources in spiders is a problem not yet completely solved by ecologists (WISE 1993). Web-building spiders have been well studied, whereas in wandering spiders, the first evidence of the existence of exploitative competition was found few years ago in an experiment with *Schizocosa ocreata* (Hentz) (WISE & WAGNER 1992).

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Competition by territorial interference has been successfully studied in the field with *Agelenopsis aperta* (Gertsch), a sheet web spider (RIECHERT 1981, 1982), but in wandering spiders there is little field evidence that this pattern is happening. We found indirect evidence for the existence of interference competition in burrowing lycosids. This is based on phenological data and spatial distribution in a population of *Lycosa tarentula fasciiventris* (Dufour, 1835). We discuss the possible role of such a competition in the study population, taking as a basis field data and a preliminary model based on Cox proportional hazards regression (COX 1972, MUENCHOW 1986).

MATERIAL AND METHODS

The study was carried out in the "Parc Natural del MassÍs de Garraf", in South of Barcelona. The area is a maquis (typically Mediterranean shrub vegetation community, 0.5–2 in height) of kermes oak (*Quercus coccifera* L.) and Pistachio (*Pistacia lentiscus* L.) with a dominance of the former.

A plot of 540 m^2 was defined and all burrows monitored fortnightly (from late August 1992 to August 1993). At each visit, Cartesian co-ordinates of the new burrows were measured, the burrowers were extracted, and the prosoma width and length, and the patella + tibia length of their right foreleg were measured. The developmental stage of each spider was recorded on every occasion (juvenile, male, subadult male, female or subadult female). The animals were extracted by inserting a thin wire in the burrow's mouth and shaking gently. When this was done, the spider left the burrow suddenly, and could be collected in a vial. They were measured in a small mesh bag and marked on the legs with enamel. The mark was replaced after moulting. Then each individual was released into the burrow using a funnel. A colour code was used to identify every individual for monitoring until the next moult.

The study species needs almost two years to reach adulthood (FERNANDEZ-MONTRAVETA *et al.* 1991, ORTA *et al.* 1993), and females can reproduce both in that year and in the next (ORTA *et al.* 1993) like other species (MCQUEEN 1978). In this way, generations overlap and 4 cohorts can co-occur in October (recently dispersed spiderlings, one-year-old juveniles, first-year reproductive females and second-year reproductive females). Contrary to what happens in other populations of this species (e.g. FERNANDEZ-MONTRAVETA *et al.* 1991), most juveniles do not establish themselves until they are one year old or more. Two burrows of juveniles less than one year old were detected, and they were not included in this analysis. The cohort of one-year-old juvenile burrowers has been studied in more detail. Data on population dynamics refer only to burrowers.

A preliminary model to test the possible existence of interference competition

With the present model we sought to disentangle the variables that could determine the time that one-year-old juveniles remained in their burrows, since the abandonment rate was quite high (fig. 3). We developed a preliminary model based on Cox proportional hazards regression (COX 1972, MUENCHOW 1986) to see what

variables influence the residence time of young spiders. The dependent variable in survival analysis is "time until an event occurs". In this case, the event was "to leave the burrow". We assumed that the site tenacity of each individual was influenced by their nearest neighbours. The neighbours considered were the ones that shared Thiessen polygon boundaries longer than 50 cm with the focal individual, because they would have a high probability of encounter with the later (arrows in figure 1 show the nearest neighbours of individual A as an example). While focal individuals were only one-year-old juveniles, 'potential influencing neighbours' included first year reproductive females as well. Second year reproductive females were discarded: we expected a weak influence of these females upon juvenile burrowers since by the time the data were collected they were too old and died during the winter.

We used two independent variables in the model:

- Q_t - Ratio between the prosoma length of the focal individual and the average prosoma length of their neighbours in the date of sample t. This ratio indicates the size of the focal individual relative to its neighbours. So, it is an index of the probability of win in an encounter with other territory holders. For each animal, the mean of this index (Q) among all the sample dates in which it was present was used. This is because neighbour individuals can change across dates, due to the high rate of leaving burrows.

- A_t - The area of the Thiessen polygon of the focal individual at the sample date t. This area can be considered the potential territory of each individual (Diggle 1983, Kenkel *et al.* 1989). To avoid edge effects, we have considered it convenient not to eliminate the polygons partially bounded with an edge of the study area, nor any interior polygons (Kenkel *et al.* 1989), because the sample would be enormously reduced. In order to counteract this error and to adjust the model to the real spatial heterogeneity, we have eliminated in each Thiessen polygon the potentially non defensible area; that is, the area occupied by bushes and rocks, where no spider could place its burrow (Barrientos *et al.* 1994) (fig. 1). To draw this area, a grid of 3x3 m was built in the field and all the elements where we expected the spider would not place the burrow were drawn. The elements with a diameter smaller than 25 cm were discarded. This area was drawn a year before the study, and their suitability for burrow settlement demonstrated a year later (Barrientos *et al.* 1994). In figure 1 we see the theoretically available area corresponds quite neatly with the area occupied by the burrows of the present study. To subtract and recalculate the exclusion area from the available one we have used the IDRISI package. We used the mean of the index among sample dates (A), as in the above variable.

The dependent variable ('time until the focal individual leaves the burrow') was measured as the sum of fortnightly time intervals when the animal was present (discrete case of Cox proportional hazards regression). The criterion to decide whether or not the burrow were abandoned, was the failure of spider extraction in consecutive sample dates, and the previous evidence that burrow maintenance (that is

to clean the burrow's mouth) had been stopped by the spider; rubbish that fell down the burrow had not been removed.

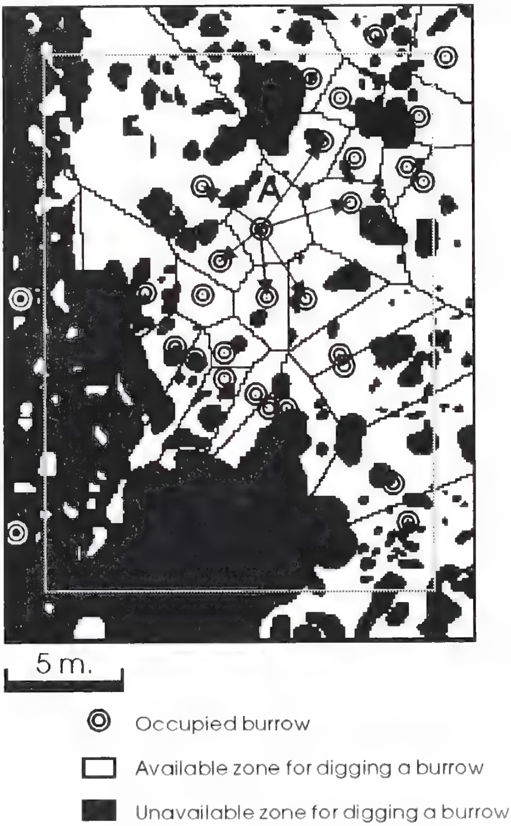

FIG. 1

Map of the study plot. The internal frame shows the area considered avoiding edge effects when calculating the nearest neighbour distances. In black is the area unavailable for burrow placement (shrubs and rocks) and discarded in the calculations of Thiessen polygon areas, in white the available area. Focal individual A is used as an example to explain the two independent variables in the Cox regression model (see text).

The theoretical model of proportional hazards is as follows:

$$h(t, Q, A) = h_0(t)\exp(\beta_1 Q + \beta_2 A)$$

Where β_1 and β_2 are coefficients of Q and A respectively and $h_0(t)$ is an unknown initial hazard function of each individual. A Chi-square test (log-likelihood method) was used to fit this model.

Nearest neighbour distance

We have applied the method of nearest neighbour distances (CLARK & EVANS 1954) to the spatial plots of almost all the sampling dates, to see if the distributions are as regular as we would expect in a territorial system (DAVIES 1978, BURGESS & UETZ 1982). To minimise the edge effects (SINCLAIR 1985), we have not considered as focal individuals the ones within an area of 2 m from the edge (fig. 1). This analysis includes as focal individuals all the animals that occupied a burrow (adults and juveniles). A simple program in C language, working with Euclidean distances from the Cartesian coordinates of the burrows, has been implemented for calculations (BURGESS & UETZ 1982). To calculate the expected distances, the total area of the plot should be used, but, since the suitable habitat seems to be restricted (BARRIENTOS *et al.* 1994), we decided to calculate the expected distances considering only the available area within the subplot resulted after subtracting the 2 m edges (173 m^2, fig. 1). As an indirect evidence of territoriality (DAVIES 1978), we expected to find a regular distribution within such area.

RESULTS

Burrow Occupation Dynamics

There were two periods of burrow settlement during the study (fig. 2 and fig. 3). The first one appeared in September, just when the spiderlings were hatched and were on top of their mother (ORTA *et al.* 1993). The second appeared in early August, just after the adult males left their burrows (fig. 3). The individuals that established their burrows in September–October were used in the Cox model, and they became adults in June. The spiders that set up the burrows in August were a later cohort found in the last sampling date, so no monitoring was established for them. The failure of juvenile burrowers before the reproductive season (June) was followed by a similar rate of recruitment (fig. 3).

Fitting the Model

To make the model fit we have included the sampling dates from September 1992 to the beginning of June 1993, when the males reached maturity and left their burrows searching for mates, and became impossible to monitor. The result is:

$$h(t, Q, A) = h0(t)\exp(-2.08\bar{Q} + 0.07\bar{A})$$

(Chi-square $\chi^2 = 11.4$, 2 d.f., $p < 0.005$, $n = 61$). The value of β_1 is negative, indicating that the smaller the focal individual was relative to their neighbours, the higher the probability of abandoning its burrow. The value of β_2 is positive, so the larger the potential territory of the focal individual, the higher the probability of abandoning its burrow.

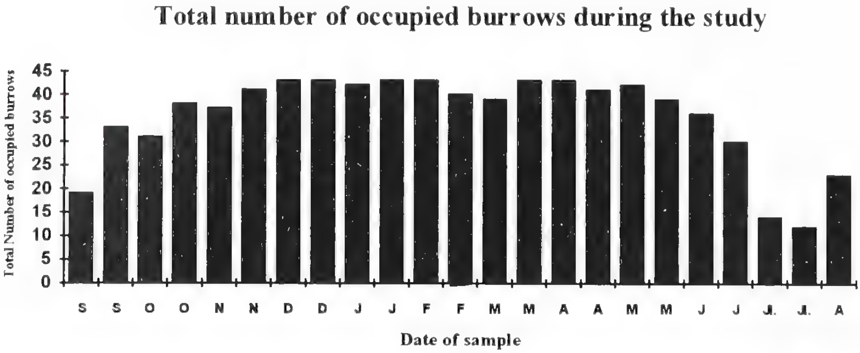

FIG. 2

Total number of occupied burrows in each sample date (1992–1993). There were new entries of one-year-old juveniles in September and in August. The decrease of burrowers in July was when all the juvenile burrowers reached adulthood and the males left their burrows searching for females (see also fig. 3).

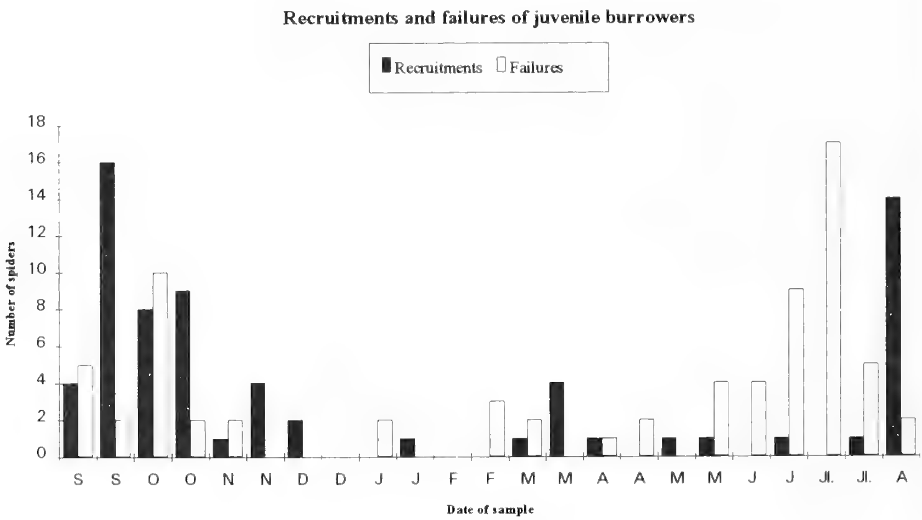

FIG. 3

Note that the number of juveniles that left their burrows during September–October, never is larger than the number of new settlers before winter. Two peaks of burrow settlement are clear (September and August).

Nearest Neighbour Distance

The results of the nearest neighbour analysis for each sampling date are shown in table I. The dates corresponding with early and mid July have been discarded because males left their burrows looking for females. Due to a new settlement of burrows in early August, this sample has been analysed (fig. 3). Although sampling dates are not statistically independent, individuals are evenly distributed within the available area during almost the whole year.

Date	n	r_a	R	C	p
A	11	2.38	1 2	1 27	N S
S	12	2 74	1 44	2 92	0 025*
S	24	1 68	1 25	2 38	0 025*
O	26	1 44	1 11	1 1	N S
O	31	1 41	1 19	2 04	0 025*
N	31	1.56	1.32	3.42	0 001**
N	33	1 46	1 28	3 11	0 001**
D	34	1.45	1.29	3.18	0 001**
D	34	1.45	1.29	3 18	0 001**
J	33	1 41	1 23	2 51	0 025*
J	34	1 37	1 21	2 35	0 025*
F	34	1.37	1.21	2 35	0.025*
F	31	1 3	1 1	1 06	N S
M	31	1.37	1 16	1 68	N S
M	35	1 42	1.27	3.1	0 005*
A	34	1 53	1 35	3.93	0 0001 ***
A	33	1.5	1.31	3 41	0 001**
M	33	1.47	1 29	3 15	0 001**
M	30	1.61	1.34	3 56	0 001**
J	28	1.45	1.17	1.67	N S
J	23	1.61	1.18	1 62	N.S
Jl	-	-	-	-	-
Jl	-	-	-	-	-
A	18	1 98	1 28	2 27	0.025*

TABLE I

Results of the nearest neighbour analysis in each sample date within the available area (white in fig. 1). The samples are not independent of each other. If $R > 1$ and $p < 0.05$ the spatial distribution is significantly regular. There is a trend towards a regular distribution across the samples.

DISCUSSION

The two periods of juvenile maximum recruitment into the burrows can be explained by a lack of competition. In September, the spiderlings have already hatched, and the females may have allowed the juveniles to install themselves in their burrows, since they had a lower energy demand due to the end of the yolking period, and would have reduced their territorial behaviour. Until then, the juveniles would have survived in the population as floaters. The existence of floaters has been described in *Agelenopsis aperta* (Gertsch) (RIECHERT 1981). In August, the males had just abandoned their burrows searching for females, creating new areas with no competition, that would be used by floaters to establish their burrows. What happens between August and September has not been studied, but we can expect an important reduction in the number of established animals to occur. This would be the result of competition with females during this period, when they are yolking eggs and need a high rate of food intake. Other authors (FERNANDEZ-MONTRAVETA *et al.* 1991) have suggested that in this period, the spatial structure of the population is determined by females. This would support the hypothesis that competition increases during the time that females are building up stores for eggs.

The rest of the year, the burrow number did not change, presumably because the disappearances coincided with new recruitments. This suggests that what happened was a burrow relocation by the animals that left their previous one. Unfortunately, we have only observed two marked juveniles that had changed their burrows. The rest of recruitments observed during the year, of course, could be explained by animals that had changed their burrow and moulted simultaneously. In periods when this recruitment and failure pattern appears repeatedly (mainly in October), it would be convenient to carry out a more exhaustive monitoring to follow the recruitment and failure more closely. According to the model, the probability that a spider leaves its burrow, when it has not done so before, depends on its potential territory size and its relative size with respect to its neighbours' size. This could be evidence of density-dependent burrow leaving and thus of interference competition. The existence of floaters, demonstrated in an indirect way during the observation of the recruitment periods, seems to indicate that the burrow-sites are a limited resource in our population. The analyses of the nearest neighbour distances show that the spiders keep a regular distribution, that could be an indication of the existence of territoriality (DAVIES 1978). We can conclude that in this population, the role of interference competition on the numbers of juvenile burrowers could be important. Thus, burrowing wolf spiders appear to be an important source for investigating the Competitionist Paradigm in wandering spiders. Future research for improving this model is needed.

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Spiders as indicator species : lessons from two case studies

Cornelis R. NEET
Centre de conservation de la faune et de la nature (Etat de Vaud)
1 ch. du Marquisat, CH-1025 Saint-Sulpice, Switzerland.

Spiders as indicator species: lessons from two case studies. - Spiders have been used as indicator species in at least two ways. The first approach examines spiders at the species level, using known ecological preferences in order to determine how spider communities react to environmental change or disturbance. In the second approach, species richness of spider communities is used as a synthetic indicator of the quality of natural habitats. An example for the first approach is the analysis of the tyrphobiont species of a series of European peat-bogs; the second approach is illustrated by the analysis of a case study on the effect of reed bed burning and mowing on species richnesss and composition. Both case studies are discussed and the following lessons are drawn :
– when individual species are used, excellent basic information on their distribution and ecology is a prerequisite for the choice of indicator taxa;
– a high standard in sampling design is needed for indicator species applications;
– precise definition of the kinds of perturbations that are expected to influence the indicator taxa is to be recommended.

Key-words: indicator species - Arachnida - Araneae - conservation - community structure - sampling design.

INTRODUCTION

For environmental applications, spiders have been used as indicator species in at least two ways. The first approach examines spiders at the species level, using known ecological preferences of species in order to determine how spider communities react to environmental change or disturbance. This approach is illustrated by the work of Buchar (1983), Maelfait *et al.* (1990), McIver *et al.* (1990) and Platen (1993). In the second approach, species richness of spider communities is used as a

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synthetic indicator of the quality of natural habitats (ALLRED 1975; KROMP & STEINBERGER 1992; POZZI 1994). A study by CLAUSEN (1986) on use of spiders for the monitoring of pollutants can also be associated with this second approach.

While most authors agree that spiders should be appropriate as ecological indicators (ALLRED 1975; BUCHAR 1983; MAELFAIT & BAERT 1988*a*, *b*; MAELFAIT *et al.* 1990; MCIVER *et al.* 1990; FÜRST *et al.* 1993; PLATEN 1993), only very few studies report supportive evidence in the context of applied ecological questions or environmental impact assessment procedures (MAELFAIT & BAERT 1988*b*; MAELFAIT *et al.* 1990; POZZI 1994). Moreover, no study has so far critically examined the limitations in the use of spiders as ecological indicators. Therefore, this work examines two case studies in order to improve the answers to the following questions:

- can spiders be successfully used as ecological indicator species ?
- what are the advantages and limitations in the use of spiders as indicator species ?
- which conditions should be fullfilled in order to develop standard use of spiders as ecological indicators ?

FIRST CASE STUDY: THE INDICATOR VALUE OF TYRPHOBIONT SPECIES

The term tyrphobiont was coined by PEUS (1928) to define species living only in peat-bogs and mires. Reviewing a series of papers dealing with the spider fauna of European peat-bogs, CASEMIR (1976) lists 8 tyrphobiont spider species: *Heliophanus dampfi*, *Pirata uliginosus*, *Clubiona norvegica*, *Theonoë minutissima*, *Aphileta (Hillhousia) misera*, *Drepanotylus uncatus*, *Hilaira excisa* and *Maro lepidus*. As peat-bogs are nowadays often perturbated or altered by exploitation, pollution or inappropriate management, one may expect to use such tyrphobiont species as indicators of good-state peat-bogs.

MATERIALS AND METHODS

This brief analysis is based on a review of published reports on peat bog spiders (11 papers were examined). Lists of tyrphobiont species and general characteristics of seven European peat-bogs were retained from papers having sufficiently complete informations for data analysis (area, state of the habitat). The state of each peat-bog was estimated from published information and defined as having a low or high level of degradation and a low or high level of geographic isolation.

RESULTS

Table 1 illustrates the number of tyrphobiont species found in the seven peat-bogs. It appears that most published studies were carried out on lowly modified peat-bogs and that the two smaller and degradated or isolated peat-bogs have fewer tyrphobiont species than the five larger and well-conserved peat-bogs (Wilcoxon signed-rank $z = -1.706$, one-tailed $p < 0.05$). However, as shown in Fig. 1, there is a

TABLE 1

Number of tyrphobiont spider species (n) found in seven European peat-bogs, with habitat area (S) and estimated state (level of habitat degradation D : low or high; level of habitat isolation I : low or high).

n	S (ha)	state (D/I)	country	reference
0	5	low/high	Switzerland	Holzapfel (1937)
2	50	high/high	Switzerland	Mulhauser *et al.* (1987)
5	630	low/low	Germany	Rabeler (1931)
1	4000	low/low	UK	Cherret (1964)
5	10000	low/low	Belgium	Baert & Kekenbosch (1982)
8	10000	low/low	Belgium/Germany	Casemir (1976)
6	31500	low/low	Estonia	Vilbaste (1980)

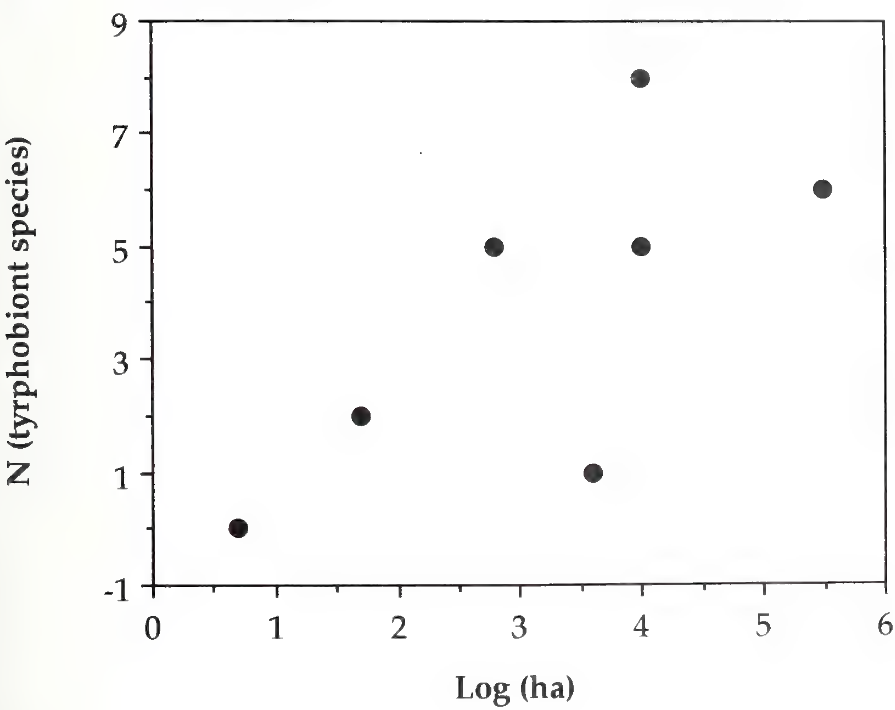

FIG. 1

Relationship between peat-bog area (Log values) and the number of tyrphobiont spider species. Kendall's rank correlation Tau = 0.65, $p < 0.05$.

significant correlation indicating that the number of tyrphobiont spiders found is directly influenced by habitat area (Kendall's rank correlation Tau = 0.65, z = 2.05, $p < 0.05$).

Discussion

The results of this simple analysis indicate that the use of tyrphobiont spiders as indicators is problematic. While the presence of tyrphobiont species is informative and may confirm that the habitat is not highly modified, the absence of such species cannot be used for assessments without care. The reason for this is that indicator species may be missing :

- because of insufficient sampling effort,
- due to the biogeographical effects of small habitat area and isolation (natural local extinctions due to the spatial and patchy distribution of the peat-bog habitats),
- because the peat-bog habitat is perturbated and altered (local extinctions due to habitat degradation and human influences).

Thus, unless one can control for the effects of habitat size and isolation and ensure appropriate sampling, it will not be possible to conclude that a peat-bog habitat is seriously modified simply because some tyrphobiont species are not found. Another more general problem regarding the use of known ecological preferences of spiders is that most species are associated with several habitat types when one considers currently used habitat classification systems. In a recent synthesis by Hänggi *et al.* (1995), which characterizes the habitats of 384 Central European species, most are found in a series of different habitats and only very few appear to be strictly associated with a given habitat type. This can be explained by the fact that spiders depend not only on microclimate and vegetation characteristics but also on the physical structure of habitats and may therefore appear in quite different habitats if appropriate physical structures are present (e.g. Duffey 1966). In the case of tyrphobiont species, although for some cases there is evidence that they are strictly related to peat-bogs, e.g. *Heliophanus dampfi* (Neet 1987), recent evidence shows for example that *Pirata uliginosus* and *Drepanotylus uncatus* also occur in other habitats (Hänggi 1987; Hänggi *et al.* 1995) and thus are not strict tyrphobionts.

SECOND CASE STUDY: THE EFFECT OF FIRE AND MOWING ON A WETLAND SPIDER COMMUNITY

An alternative to assessments based on autecological data of individual species is to look for more synthetic indicators such as species richness. The data presented here are taken from a study that was carried out in the wetlands of the natural reserve of "Les Grangettes" on the Eastern end of the Lake Leman (Switzerland). Invertebrates were collected in order to assess the effects of a fire that occured in May 1992. Since the fire affected mown and unmown areas of the reed bed, this analysis examines both effects of burning and mowing on species richness and composition.

MATERIALS AND METHODS

The sampling design included four sampling sites organized as follows.

Site 1 : control plot 1, burned plot 1; Site 2 : control plot 2, burned plot 2; Site 3 : mown plot 1, burned & mown plot 1 ; Site 4 : mown plot 2, burned & mown plot 2. In site 4, there was also an intermediate plot between the two other ones. Hereafter, "burnt" and "mown" are considered as two treatments. All sites were situated along one border of a large burnt area of 30 ha, with a more or less uniform cover of *Phragmites australis*, *Carex lasiocarpa* and *C. elata*; the sites 1 and 2, which were not mown, included dense patches of *Carex* sp. The distance between sites varied between 60 and 200 m. Sites were situated at increasing distances from the Lake Leman, site 1 being closest to the lake and site 4 most distant. On each plot 6 pitfall and 2 emergence traps were placed. Sampling started 5 days after the fire and specimens were collected every 7 days during 9 periods (from May to September 1992). A detailed report on the study site (HOFMANN *et al.* 1994), as well as an analysis of the spider fauna, with detailed species lists and different analyses at the species level (ECOCONSEIL 1994) are available.

TABLE 2

Total species richness and number of species per family for the most abundant spider families according to different treatments of the habitat (tests after SIEGEL & CASTELLAN 1988)

	Treatment				
	No*	Burnt	Mown	B+M**	test (Fisher exact or Chi-square)
Species richness :					
Total	35	33	38	36	Chi-square = 0.53 NS
Araneidae	3	2	2	0	Fisher ex. = 0.52 NS
Clubionidae	5	4	2	4	Fisher ex. = 0.61 NS
Linyphiidae	8	5	12	10	Chi-square = 7.0 $p < 0.01$
Lycosidae	6	8	10	10	Chi-square = 3.2 NS
Salticidae	3	4	2	5	Fisher ex. = 1.00 NS

* Control **Burnt and Mown

RESULTS

Table 2 indicates that total species richness did not differ between the different treatments. Among the most abundant families, a significant difference in species richness per family was found only for Linyphiidae, where the effect of mowing appears to be an increase of richness.

In order to examine whether species composition was influenced by treatments, a cluster analysis of plot similarity was performed using the species abundances of each sampling plot as descriptors.

Following the recommandations of LEGENDRE & LEGENDRE (1979), similarity was mesured by the chi-square distance and the UPGMA clustering method was

selected (Fig. 2). The plots are grouped according to spatial proximity rather than to treatment, indicating that the spatial distribution of the plots has a major influence on species composition. A Mantel test (MANLY 1986) was used to evaluate this indication, by estimating the correlation between the similarity matrix and inter-plot distance classes (distance matrix). Among the four distance classes tested (one intrasite and three intersite), only one intersite distance class is significantly correlated with similarity ($r = -0.59$ $p < 0.05$). This suggests the presence of a spatial structure in the data, i.e. differences between sampling sites related to spatial position.

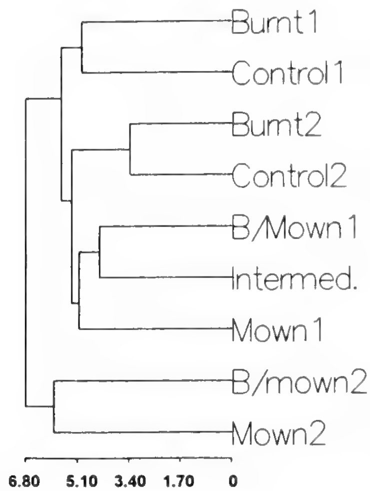

FIG. 2

Cluster analysis of plot similarity using species abundances as descriptors (Chi-square distance and UPGMA clustering).

These results show that treatments did only affect richness of some groups of species (Linyphiidae) without affecting total richness and without deeply modifing community structure. An important aspect was unfortunately not taken into consideration in the sampling design: water level. In wetlands situated on lakeshores, when sampling occurs over several weeks, the water level may vary and influence species richness on local plots as well as pitfall trapping efficiency. Given the positions of sampling sites, a gradient of water level is one of the probable factors that may explain the spatial structure detected in the data.

DISCUSSION

The conclusion that burning or mowing did not globally diminish species richness is consistent with the results obtained by DITLHOGO *et al.* (1992), who showed that total number of invertebrates, species-richness, diversity and evenness

show no relationship with cutting or burning reed-beds. USHER & SMART (1988) have even found increases of species richness after a heathland fire. From the results presented here, one could thus conclude that spider species richness can be used as an indicator of the non-harming effect (no reduction of species richness) of burning and mowing. This kind of conclusion has important practical consequences as reed bed mowing and protection against fire are current issues for local managers. However, alternative interpretations can be found :

- the results could be biased if sampling insufficiently covered species living in the upper layers of the herbaceous cover (Araneidae, Clubionidae); therefore some important components of species richness and composition may have been missed,
- the presence of a spatial structure in the data indicates that uncontrolled factors such as the influence of water level may affect sampling design and results,
- if, after the treatments, some species are definitely lost and others newly invading the community, effects on species richness may be delayed in time due amongst other reasons to modifications in interspecific interactions.

Delayed effects have actually been found by MERRETT (1976) who noticed an evolution of community composition over ten years after heathland fires. Therefore, species richness alone as an indicator could be somewhat limited : if species richness remains constant but with ordinary species progressively replacing rare ones, the effect would actually be negative for conservation.

CONCLUSIONS

Returning to the questions of the introduction, following answers can be suggested. First, there is evidence that spiders can be used as ecological indicators (see also MAELFAIT & BAERT 1988*a* and MULHAUSER 1990 for other discussions). Besides published results mentioned above, the non-harming effect of reed-bed burning and mowing is an illustrative example. Advantages of spiders as ecological indicators are their abundance in all ecosystems, the fairly easy identification and, as predators, their integrative trophic level. One major disadvantage is the limited association between currently used habitat classifications and the actual patterns of spider habitat selection, resulting in a very limited number of spider species selecting a unique habitat (HÄNGGI *et al.* 1995), even in the case of presumable habitat specialists such as tyrphobionts. Regarding limitations in the use of spiders as indicators and the conditions which should be fullfilled in order to develop standard use of spiders as ecological indicators, the following lessons can be drawn from the examples presented here :

- when individual species are used, the availability of excellent basic information on their distribution and ecology cannot be overlooked and should be considered as an important prerequisite for the choice of indicator taxa,
- a high standard in sampling design is needed, in order to control as much as possible for confounding situations and alternative explanations to the patterns observed.

The interest of ecological indicators is to replace very detailed studies of community ecology by simplified approaches that permit to organize monitoring over larger spatial and time-scales. To monitor river ecosystem pollution such tools have been develop with success, in particular due to the fact that the perturbation under test is clearly defined and has obvious detrimental consequences (water pollution). If terrestrial indicators are to be used in practice, a last recommandation would therefore be to take care to define exactly what kind of perturbations are under test and which are their expected consequences. This will help clarifying problems of sampling design by clearly separating the different effects that may occur simultaneously, as in the peat-bog example where habitat isolation and habitat degradation by exploitation may occur, or in the second case study, where an important factor such as water level was not controlled for.

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Prey specificity of the venom of the ctenid spider *Cupiennius salei* (Araneae, Ctenidae)

Wolfgang NENTWIG & Andreas BÜCHELER
Zoological Institute, University of Berne
Baltzerstr. 3
CH-3012 Berne, Switzerland

Prey specificity of the venom of the ctenid spider *Cupiennius salei* **(Araneae, Ctenidae).** - The extremely different susceptibility of arthropods to the venom of *C. salei* is explained by a varying K+/Na+ ratio or by different contents of taurine or histamine or other synergistic resp. inhibitive substances in the hemolymph of the target prey items.

Key-words: Spider venom – peptide toxins – LD 50 – prey selectivity.

INTRODUCTION

The ctenid spider Cupiennius salei is a polyphagous species. It preys under natural conditions – as far as the few observations can be generalised – on a wide spectrum of prey items (BARTH & SEYFARTH 1979). Feeding experiments under laboratory conditions with a wide range of potential prey groups in Europe confirm these results and show *C. salei* to have the widest feeding niche breadth among 6 families of wandering spiders tested (NENTWIG 1986). With this knowledge one would expect that the venom of this spider acts on a wide range of arthropods in a more or less similar manner. First tests of the sensitivity of arthropods to the venom of *C. salei* showed, however, that there are large differences among several common prey taxa (STUDER & NENTWIG 1993). Since these unexpected results could even suggest a specialisation of the venom we present here some results and interpretations which may help to understand such a contradictory situation.

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MATERIAL AND METHODS

To investigate the effect of the venom of *C. salei* on insects we regularly milked venom from our laboratory stock. By injecting various amounts of this venom into insects we got a measure for the susceptibility of the insects to the spider venom. The calculated LD 50, that is the lethal dose of venom which kills 50% of the experimental group, is a common figure to do such comparisons. Technical aspects of spider rearing, biochemical venom analysis and LD 50 are described in MALLI *et al.* (1991) and KUHN-NENTWIG *et al.* (1994).

RESULTS AND DISCUSSION

Our tests with 20 arthropod and one vertebrate species show that the *C. salei* venom is effective in all cases but we found remarkable differences in the susceptibility of the investigated animals. They cover a range of 5 log units with white mice and flies being the most sensitive animals (LD 50 < 0.02 nl crude venom per mg body weight) and some roaches, beetles and ants being very resistant (> 4 nl venom, highest value 24 nl). Many other groups (most roaches, spiders, isopods, stick insects, moths, lacewings and crickets) are in between. There are several ways to explain these results.

Prey palatability. One possible interpretation could be that the venom had been developed or evolved by the spider to subdue the most suitable prey groups and that those taxa which are no good food are less sensitive because the venom had not been evolved for them. Feeding experiments, however, show that the acceptance rate does not explain the wide range of LD 50 values. Some ants (*Formica rufa*, *Lasius niger*, *Messor rufitarsis*, *Myrmica* sp.) and beetles (*Agelastica alni*, *Tenebrio molitor*) which demand high doses of venom are eaten by *C. salei* only at medium or even low acceptance rates. At least 4 arthropod groups (the roaches *Blaberus* sp., *Blatta orientalis* and *Nauphoeta cinerea*, the crickets *Acheta domesticus*, *Gryllus* sp. and *Grillodes sigillatus*, the stick insects *Carausius morosus* and the spiders *Cupiennius salei* itself), however, are in the same susceptibility range and represent highly acceptable prey items. The nearly always refused lacewing *Chrysoperla carnea* counts among the medium sensitive insects. Additionally, characters such as ,"suitable" or "palatable" are difficult to interpret since they do not represent a physiological mechanism for venom resistance.

Ion concentration in the insect hemolymph. The most active toxin in the venom of C. salei CSTX-1, is inhibited by K+ but not by Na+. So, high K+ concentrations prevent envenomation, and a varying ratio of K+ to Na+ in an insect hemolymph can be a possible explanation for the different susceptibility of these arthropods. Most insects which have a medium to high K+ concentration (e.g. the crickets *Acheta domesticus* and *Gryllus* sp., the stick insect *Carausius morosus*. *Cupiennius salei* itself, the roach *Nauphoeta cinerea* and the ant *Formica rufa*) are also less sensitive to

the toxin. Additionally, there are some within-group effects which can be explained by this overall scheme. Two cricket species (*Acheta domesticus* and *Gryllus* sp.) e.g., have a high K+ concentration and show a high LD 50 value (this means that they are relatively venom resistant), but a third cricket species (*Grillodes sigillatus*), the most sensitive one) has a low K+ concentration (which would explain its toxin sensitivity).

A good correlation for all arthropods does neither exist for K+ nor for Na+, probably because the physiology of insects is too different. The ratio K+/Na+, however, yields a more uniform value which is considerably good correlated with the sensitivity (measured as LD 50) ($Y = 14.092 / (x + 1.032)$, Quasi-Newton test, $p < 0.05$).

Additional synergisms. Our potassium theory gives acceptable explanations within groups but still does not explain the whole story because we find sensitive and resistant prey taxa at all LD 50 levels. We therefore searched for other substances which modulate the effects of some toxins. Since the crude venom of *C. salei* is a multicomponent system which contains a mixture of dozen of substances of differing modes of action our limited investigations have probably discovered only some of the potential effects. Beside many toxic peptides the crude venom of *C. salei* contains polyacyl amines, a hyaluronidase, histamine, several amino acids including the unusual taurine and many other low molecular substances (KUHN-NENTWIG *et al.* 1994). LD 50 biotests showed that the toxicity of CSTX-1 increases in the presence of taurine by 37% and when histamine is added by 65%. A high content of these low molecular substances (> 5 mM taurine or > 0.1 mM histamine) in an insect would for example explain a higher sensitivity to the venom. Unfortunately in most insects we do not know the taurine or histamine concentration in their hemolymphs but such investigations are in preparation.

In conclusion we think that the selectivity of the venom of *C. salei* is probably no process primarily driven by the spiders' evolutionary forces but caused by multiple physiological conditions in the prey items. The ratio of K+/Na+ (or other ions) offers some explanation possibilities, but other substances will certainly add to this effect. These can be taurine and histamine but also further hitherto unidentified substances may show additional synergistic effects.

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Precopulatory male ethograms of three species of *Lycosa* Latreille 1804 (Araneae: Lycosidae) of the Iberian peninsula

Juan Manuel ORTA-OCAÑA, Jordi MOYA-LARAÑO & José A. BARRIENTOS
Unitat de Zoologia. Departament de Biologia Animal, Biologia Vegetal i Ecologia. Universitat Autònoma de Barcelona. E-08193 Bellaterra (Barcelona), Spain.

Precopulatory male ethograms of three species of *Lycosa* Latreille, 1804 (Araneae: Lycosidae) of the Iberian peninsula. - In order to revise the representatives of the genus Lycosa from the Iberian Peninsula, the courtship behaviour of the males of the three morphotypes was analysed from a total of 46 male-female interactions. The three ethograms presented here are subdivided into four parts: locomotory behaviours, foreleg movements and postures, palpal movements and postures and other behaviours. From the qualitative analysis of the repertoires, several differences in movements and postures can be seen, so we can conclude that the three morphotypes can be considered as three different species. While *L. radiata* shows extensions with vibration, *L. tarentula fasciiventris* shows static extensions and arches. There also are differences in the palpal movements. *Lycosa* sp. shows exclusive behaviours such as flexions, foreleg balance and sudden advances, as well as behaviours also seen in *L. radiata* and *L. tarentula fasciiventris*.

Key-words: *Lycosa tarentula fasciiventris* - *Lycosa radiata* - *Lycosa* sp. - ethogram- courtship - isolation mechanisms - biospecies.

INTRODUCTION

This study is part of a project aiming to revise taxonomically the genus *Lycosa* in the Iberian Peninsula using behavioural and ecological criteria, as well as the classical morphological ones. The representatives of the genus *Lycosa* in the Iberian Peninsula are *Lycosa radiata* Latreille, 1817 and *L. tarentula fasciiventris* Dufour, 1835. Nevertheless, new morphotypes that do not fit into either of these two species have been found.

The genus *Lycosa*, which names the family Lycosidae, comprises 116 species distributed over the hot and temperate regions of the World. Nearly 20 nominal species have been recorded from the Iberian Peninsula, although their biological

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entity is questionable. Following BARRIENTOS (1981), we can conclude that only two of them can be considered as biological species: *Lycosa radiata* Latreille, 1817 and *L. tarentula fasciiventris* Dufour, 1835. Nevertheless, new morphotypes (*Lycosa* sp.) have been found that do not fit in any of the accepted forms. So, a revision of the genus is necessary, bearing in mind the species concept in a wider point of view than the one given by taxonomy on its own.

The biological species concept requires the existence of isolation mechanisms to guarantee the existence of separated species. The ethological barriers may be regarded as the most important isolating mechanisms (MAYR 1970). Lycosidae is a morphologically homogeneous group and due to the fact that the species we are studying are syntopic, the ethological mechanisms might explain the speciation processes in the group.

Ethological barriers are due to behavioural incompatibilities. The male of one species performs some courtship patterns that are recognised just by the adequate female. These mechanisms have been observed in a vast group of insects and spiders. The validity of these ethological patterns as isolation mechanisms has already been proved in other *Lycosa* species (COSTA & CAPOSACALE 1984; COSTA & FRANCESCOLI 1991), as well as in many other lycosid species (UETZ & STRATTON (1982), *Schizocosa* spp.) and other families (VLIJM 1986).

MATERIAL AND METHODS

The spiders were collected as juveniles from different populations in the Barcelona area and kept in isolated cages. After becoming adults, male-female pairs were chosen at random and the female put into the observation cage 24h prior the introduction of the corresponding male. Observation cages were made of transparent plastic and consist in two adjacent areas of 15 x 15 cm. separated by a removable opaque barrier. This barrier was removed at the beginning of the experiment. The interactions were recorded on video tape for further analyses.

After 22.5 hours of observation, we constructed three ethograms of the different movements and postures of the three forms. Some of the terms used in the ethograms were taken from the literature (NOSSEK & ROVNER 1984; ASPEY 1977). Within those 22.5 hours, 26 male-female interactions were recorded for *L. radiata* (409 min), 13 interactions for *L. tarentula fasciiventris* (502 min) and 17 for *Lycosa* sp. (440 min).

RESULTS

Due to the fact that there are a lot of details that can be recorded in one interaction, we have divided the ethogram in different subrepertoires, to allow the independence of the categories in each subrepertoire. The categories can overlap between subrepertoires, but not in the same subrepertoire. So, different observers could record different subrepertoires or the same observer could record different

subrepertoires in different video reviewing sessions. At the end of the sessions, it would be possible to obtain a multiple behaviour chart. We have only elaborated the male's premating ethogram, although we are aware of the relevant importance of the female's behaviour, so ethograms should be elaborated for the latter.

1. Locomotory behaviours

Common behaviours

1.1. Stationary: the male remains motionless, with the four pairs of legs in contact with the substrate.
1.2. Approach: the male advances so it reduces the distance between itself and the female.
1.3. Retreat: the male moves away so it increases the distance between itself and the other one. It is assumed that the other spider is stationary. It is possible that the female goes after the male, so there is no actual increase in the distance between them.
1.4. Orientation: the male turns around an imaginary vertical axe so as to end up facing the female.
1.5. Side movement: the male moves towards its right or left side, without displacement forward or backwards.
1.6. Step-Wave: hyperextension of one or typically both legs I and II during forward motion. At the top of the raise, the femora are held at an angle of 40-60° relative to the substrate. Forward motion continues as the forelegs are lowered to the substrate and again hyperextended and raised.
1.7. Random activity: running without an specific orientation.

L. tarentula fasciiventris **exclusive behaviours**

1.8. Side movement around the burrow: similar to the previous category (1.5), but with the burrow as the centre of the side movement.

Lycosa **sp. exclusive behaviours**

1.9. Fast approach: the spider advances very quickly reducing the distance between itself and the female..

2. Foreleg movements and postures

Common behaviours

2.1. Stationary: the leg is in contact with the substrate.
2.2. Horizontal extend (left/right/both): the extended leg is raised and held parallel to the substrate. (fig. 1. a) (not in *L. tarentula fasciiventris*).

2.3. Oblique extend (left/right/both): the leg is extended straight, the femur is held at an angle of 45-60° relative to the substrate. (fig. 1. b)

2.4. Vertical extend (left/right/both): the leg is extended straight and the femur is held at an angle of 60-90° relative to the substrate. (fig. 1. c)

L. radiata exclusive behaviours

In categories 2.2 to 2.4, it is common to observe some vibration of the legs raised. This vibration is not quantified in the ethogram.

2.5. Tapping (left/right/both): the leg is raised straight about 30-40° relative to the substrate and subsequently lowered to contact the substrate, as if it were probing the substrate. It is similar to 2.2 but here the tip of the leg touches the substrate or silk threads (laid by the female). (fig. 1. d)

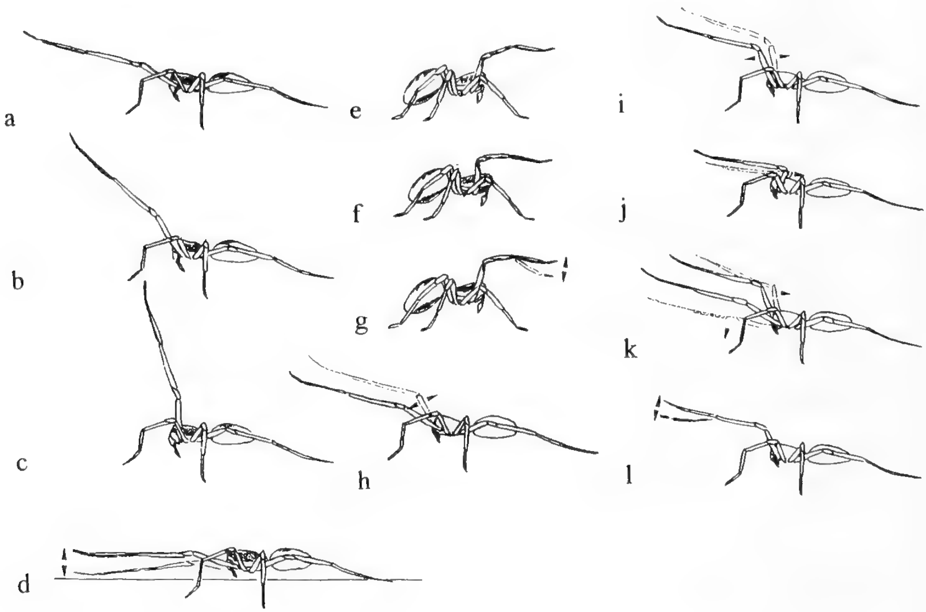

FIG. 1

Foreleg movements and postures: Extends. a.- Horizontal extend (2.2); b.- Oblique extend (2.3); c.- Vertical extend (2.4); d.- Tapping (*L. radiata* exclusive behaviour) (2.5). Exclusive foreleg movements and postures. e.- Vertical arch (2.6); f.- Obtuse arch (2.7); g.- Arch balancing (2.8). *Lycosa* sp. exclusive foreleg movements and postures. h.- Oblique flex (2.9);i.- Vertical flex (2.10); j.- Obtuse flex (2.11); k.- Foreleg balance (2.12); l.- Metatarsal oscillation (2.14). Numbers in brackets refer to the category number in text.

TABLE I

	form / behaviour number	*Lycosa radiata*	*Lycosa tarentula fasciiventris*	*Lycosa* sp.
Locomotory behaviours	1.1 Stationary	■	■	■
	1.2 Approach	■	■	■
	1.3 Retreat	■	■	■
	1.4 Orientation	■	■	■
	1.5 Side movement	■	■	■
	1.6 Step-wave	■	■	■
	1.7 Random activity	■	■	■
	1.8 Side mov. burrow		■	
	1.9 Fast approach			■
Other behaviours	4.1 Contact	■	■	■
	4.2 Mount	■	■	■
	4.3 Retreat	■	■	■
	4.4 Mating position	■	■	■
	4.5 Female's burrow entry		■	

	form / behaviour number	*Lycosa radiata*	*Lycosa tarentula fasciiventris*	*Lycosa* sp.
Palpal movements	3.1 Stationary	■	■	■
	3.2 Palpal drumming	■	■	■
	3.3 Silk touch	■		
	3.4 Palpal drum. on the rim		■	
Foreleg movements and postures	2.1 Stationary	■	■	■
	2.2 Horizontal extend	■		■
	2.3 Oblique extend	■	■	■
	2.4 Vertical extend	■	■	■
	2.5 Tapping	■		
	2.6 Vertical arch		■	
	2.7 Obtuse arch		■	
	2.8 Arch balancing		■	■
	2.9 Oblique flex			■
	2.10 Vertical flex			■
	2.11 Obtuse flex			■
	2.12 Foreleg balancing			■
	2.13 Sudden advance			■
	2.14 Metatarsal oscillation			■

L. tarentula fasciiventris exclusive behaviours

This species doesn't show horizontal extends (category 2.2) Opposite to *L. radiata*, vibration is not observed in categories 2.3 and 2.4.

2.6. Vertical arch (left/right/both): the leg I femur is raised at 60-90° relative to the substrate, and the femoro-patellar joint is flexed, as well as the tibio-metatarsal joint, although this one is less flexed. (fig. 1. e)

2.7. Obtuse arch (left/right/both): the leg I femur is pointing posteriorly at 95-140°. The femoro-patellar joint is flexed, as well as the tibio-metatarsal joint. This category is usually seen when the male is at the female's burrow. (fig. 1. f)

2.8. Arch balancing (left/right/both): the leg is raised in one of the arch categories while is slowly moving up and downwards at the tibio-metatarsal joint. The movement is slow, it is not a vibration movement. (fig. 1. g)

In categories 2.3, 2.4 and 2.6 to 2.8, the most usual is that the spider moves both forelegs.

Lycosa sp. exclusive behaviours

In categories 2.2 to 2.4 is not usual to observe vibration. If it occurs, it is short, on the contrary as it happens in *L. radiata*. Illustrations are the same as for *L. radiata*.

2.9. Oblique flex (left/right/both): the leg I femur is raised and held at 45-60° relative to the substrate. The femoro-patellar joint is flexed, as well as the previous joints, while the rest of the leg segments remains parallel to the substrate. (fig. 1. h)

2.10. Vertical flex (left/right/both): the leg I femur is raised and held at 60-90° relative to the substrate. The femoro-patellar joint is flexed, as well as the previous joints, while the rest of the leg segments remain parallel to the substrate. (fig. 1. i)

2.11. Obtuse flex (left/right/both): the leg I femur is raised and held pointing posteriorly at 95-140° relative to the substrate. The femoro-patellar joint is flexed, as well as the previous joints, while the rest of the leg segments remains parallel or in an acute angle to the substrate. (fig. 1. j)

2.12. Foreleg balancing: While one leg is being flexed or extended at the femoro-patellar joint, the other may remain motionless or moving in an opposite way (e.g.: one leg is being extended and the other flexed). (fig. 1. k)

2.13. Sudden advance: while the forelegs are extended or flexed, the spider suddenly jumps forward, while legs II (right/left/both) are raised briefly. A brief vibration of legs is often observed prior to the jump.

2.14. Metatarsal oscillation (right/left/both): a slight oscillation at the tibia-metatarsal joint is performed. It rarely occurs. (fig. 1. l)

3. PALPAL MOVEMENTS AND POSTURES

Common behaviours

3.1. Stationary: the palps remain motionless, more or less perpendicular to the substrate.

3.2. Palpal drumming: palps alternately lifted and lowered in rapid succession, usually contacting the substrate.

L. radiata **exclusive behaviours**

3.3. Silk touch (left/right/both): the palps touch a silk thread.

L. tarentula fasciiventris **exclusive behaviours**

3.4. Palpal drumming on the rim: the palpal drumming is performed on the rim surrounding the female's burrow.

4. OTHER BEHAVIOURS

Common behaviours

4.1. Contact: one spider's foreleg (usually the male's) contacts some part of the body of the other spider.

4.2. Mount: the male climbs over the female's body but does not adopt the mating position (4.4.).

4.3. Retreat: the male moves slightly backwards.

4.4. Mating position: the male places itself in the mating position (type 3, FOELIX 1982), although actual copulation may not take place.

L. tarentula fasciiventris **exclusive behaviours**

4.5. Female's burrow entry: the male gets into the female's burrow.

DISCUSSION

In this qualitative study of courtship, we can see several differences among the species. *L. radiata* and *L. tarentula fasciiventris* show clearly different categories in the subrepertoire of leg movements and postures. While *L. radiata* shows extensions with vibration, *L. tarentula fasciiventris* shows static extensions and arches. There are also differences in the palpal movements repertoire, probably associated with other communication channels as acoustic (UETZ & STRATTON 1982; STRATTON & UETZ 1983) or chemical communication (TIETJEN & ROVNER 1980, 1982). On the other

hand, *Lycosa* sp. shows behaviours seen in *L. radiata* and *L. tarentula fasciiventris* (extensions and arch balancing), but also exclusive behaviours as flexions, foreleg balancing and sudden advance. The absence/presence of behaviours is summarised in table I. We can conclude, from a qualitative point of view, that we are dealing with a different species. A comprehensive study of the behaviour's variation is needed, as well as carrying out reproductive isolation experiments. Since sequential analyses have not been performed yet, it would be too speculative to state which of the behaviours observed may be the important in the species recognition process, this is, which one transports the signals to the female. Moreover, part of the courtship takes place via non-visual channels that haven't been analysed in the present work.

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Ecology of sexual dimorphism in spiders of the genus *Metepeira* (Araneae: Araneidae)

William H. PIEL
Museum of Comparative Zoology, Harvard University, Cambridge MA 02138, USA.

Ecology of sexual dimorphism in spiders of the genus *Metepeira* (Araneae: Araneidae). - Spiders of the genus *Metepeira* living in different habitats show inter- and intraspecific variation in degree of female aggregation. I examined sexual size dimorphism in three species of *Metepeira* in Mexico to evaluate the relationship between habitat, female aggregation, and size dimorphism. *Metepeira incrassata* lives in highly productive habitats, has almost exclusively communal females, and shows little dimorphism. In contrast, *Metepeira* species A lives in less productive habitats, has mostly solitary females, and shows a high degree of dimorphism, with males much smaller than females. Finally, *Metepeira spinipes* shows geographic variation in both female communality and sexual dimorphism. In productive habitats that promote communal females, large males predominate. In less productive habitats that promote solitary females, dwarf males predominate. In habitats that promote a mixture of colonial and solitary females, both dwarf and large males coexist. Large males appear to be adapted for competing against other males in large colonies, whereas dwarf males are adapted for traveling over land in search of solitary females.

Key-words: Sexual size dimorphism - colonial behavior - ecology - *Metepeira* - spiders.

INTRODUCTION

Many spider species show sexual dimorphism, with females larger than males (VOLLRATH 1980). Dimorphism is generally more pronounced among spiders with high male mortality which comes from the risky behavior of searching for widely spaced females (VOLLRATH & PARKER 1992). In the present study, I examined sexual dimorphism in *Metepeira* F. O. Pickard-Cambridge that vary in degree of female aggregation.

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Spiders of the genus *Metepeira* living in different habitats show variation in female aggregation (UETZ 1982). *Metepeira incrassata* Pick.-Cambr. occurs in tropical rain forests and 99% of females live in colonies with two or more individuals (UETZ 1988). In contrast, species A (species description in preparation) occur in desert mesquite grasslands and almost 80% of females live solitarily, with group size rarely exceeding ten individuals (UETZ *et al.* 1982). Finally, *Metepeira spinipes* Pick.-Cambr. is variable in both habitat and sociality. *M. spinipes* can be found in dry mesquite desert where females are almost entirely solitary, as well as more humid agricultural land around Mexico City where almost 70% live communally (UETZ *et al.* 1982). UETZ (1988) concluded that females aggregate into foraging flocks as a risk sensitive response to prey availability.

In the present study, I examined sexual size dimorphism in species A, *M. incrassata*, and *M. spinipes* to evaluate the adaptive significance of inter- and intra-specific variation.

METHODS

I collected specimens of the three *Metepeira* species, species A, *M. incrassata*, and *M. spinipes*, at 17 different sites in Mexico. I also examined specimens representing about 60 different sites, from the collections of the American Museum of Natural History, the Californian Academy of Sciences, and the Museum of Comparative Zoology.

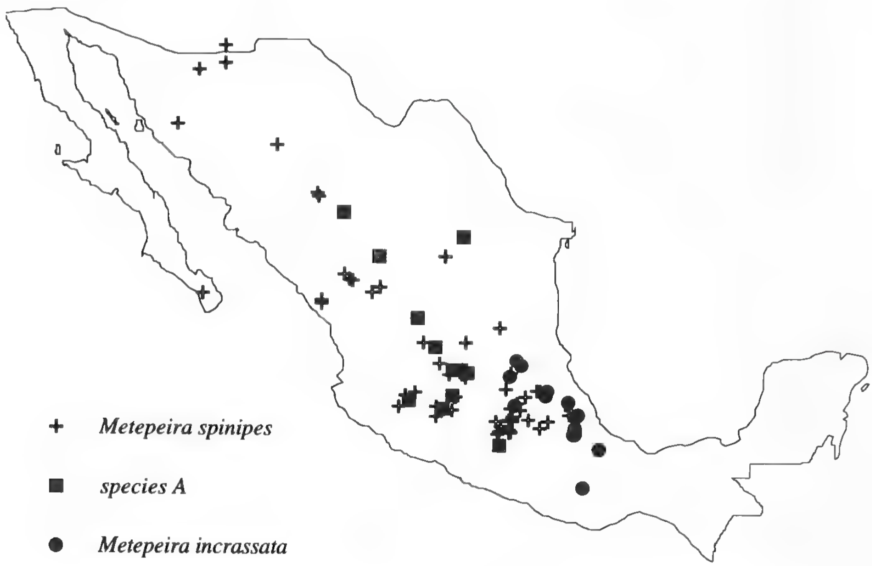

FIG. 1

Geographic distribution of three *Metepeira* species: *M. incrassata*, species A, and *M. spinipes*, in Mexico.

In my field collections, I used a Sony Pyxis GPS to determine the precise geographic coordinates and altitude of each collection site. For museum specimens, I determined the site coordinates using a USBGN Gazetteer, and site altitudes by consulting a DMAAC ONC J-24 aeronautical map.

For each specimen, I measured body length from anterior tip of the prosoma to posterior tip of the abdomen, using a dissecting microscope equipped with a reticule. For species A and *M. atascadero*, I calculated size-ratio as the body length of each male divided by the average length of all measured females of the same species. For *M. spinipes*, which showed geographic variation in female size, I calculated size-ratio as the body length of each male divided by the average female length for his locality.

RESULTS

The three species of *Metepeira* differ in their geographic distribution (Fig. 1). Species A occurs in Central Mexico, and *M. incrassata* in southern Veracruz. *M. spinipes* has a wide distribution between California and Mexico City (Fig. 1).

M. incrassata shows relatively little sexual dimorphism whereas species A shows a large degree of sexual dimorphism, with 25% of males being less than half the size of the average female (Fig. 2). *M. spinipes* displays a wide range of dimorphism, spanning those of *M. incrassata* and species A (Fig. 2). Male size in *M. spinipes* is remarkably variable. For example, in the town of Huitzilac, I found tiny *M. spinipes* males (4.2 mm) as well as large males (8.5 mm) competing for the same females (9-11

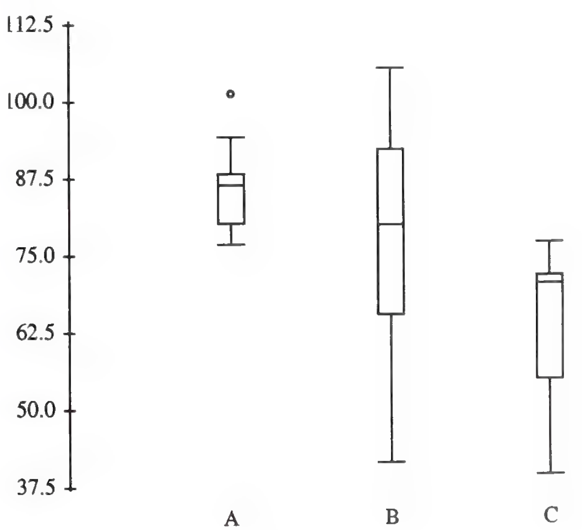

FIG. 2

Box plots of percent male size relative to average female size. A *Metepeira incrassata* (n = 21); B *Metepeira spinipes* (n = 55); C species A (n = 12).

TABLE 1

Lengths (mm) of female and male *M. incrassata*, *M. spinipes*, and Species A. Mean, maximum, and minimum values for females are: *M. incrassata*, 7.57 mm, 9.05, and 6.35 respectively; *M. spinipes*, 9.05 mm, 12.4, and 5.5; Species A, 7.92 mm, 6.0, and 9.5. Sexual size dimorphism expressed as a percent male size relative to mean female size is presented in Fig. 2.

M. incrassata (mm)		*M. spinipes* (mm)				Species A (mm)	
Female	Male	Female		Male		Female	Male
6.35	6.2	7.9	6.5	7.9	6.25	8.25	3.6
7	6.1	10.75	10	6.75	8.5	8.75	6.25
7.4	5.5	8.3	6.75	8.5	8.95	9.5	6.25
7	6.75	11.75	8.75	7.65	3	8.25	4.1
7.25	6.25	10.75	9.25	7.7	4.5	9.5	5.65
8.2	7.25	9.2	10.6	6.5	8	7.25	6.85
7.35	4.25	10	10.5	6.15	6	6	6.8
6.65	5.75	8.25	9.8	4.75	6.5	7.25	6.5
7.75	5.65	6.75	6.75	4.65	5.1	9.35	6.25
8.85	6.2	9.75	11.5	3.5	8.5	7.5	3.5
8.75	5.75	7.75	7.65	6.3	6.25	6.9	5.75
7	6.4	7.35	9	8.9	7.15	6.5	6.85
6.9	6.75	6.9	7.75	6.75	8.35		
7.35	6.75	7.2	5.5	5	5.6		
7.3	5.25	7.75	8.5	3.75	6		
8.5	7.5	10	7	10.75	9.5		
8.5	8	12	9	3.15	8.25		
8.7	6.6	12.15	11.5	3.75	6.15		
7.15	6.5	8.7	10.5	4.5	9.15		
7.1	6.25	9.15	7.5	5.3	6.5		
7.3	4.6	9.5	8.3	6.5	6.5		
7	6.2	8.5	11	5.5	8.35		
7.8		12.4	8	7.2	6.65		
8		8.8	11	4.75	7.6		
7.3		9	8.25	6.2	7.15		
7.65		8.05	10.4	7	7.7		
9.05		7.1	9.3	8.75	8.5		
7		11.5		4.25			
8.1							
7.25							
7							

mm). In fact, the smallest male *M. spinipes* I examined is only 3 mm in length, the largest 10.8 mm. Examining the effect of altitude and latitude in *M. spinipes* (Fig. 3), there appear to be three distinct regions: low altitude and low latitude localities are dominated by giant males in putatively highly social populations; high altitude and high latitudes produce dwarf males in populations of mostly solitary spiders; and high altitude, low latitude sites have a mixture of large, dwarf, and average sized males in presumably semi-communal populations. These data suggest that males engage in separate, specific strategies because the variance of sexual dimorphism in average

TABLE 2

Lengths of individual *Metepeira spinipes* males and mean lengths of *M. spinipes* females for each locality. Columns are locality (LOC) in latitude and longitude; mean lengths (mm) for all females measured from that locality (MFL); and lengths (mm) of individual males measured from that locality (LIM). Data presented in Fig. 3 are expressed as a percentage of each LIM to it's corresponding MFL.

LOC	MFL (mm)	LIM (mm)				
18°50'N 99°41'W	8.5	8				
18°55'N 99°15'W	9.8	8.9				
19°0'N 99°15'W	9.9	7.6	7.2	7.7		
19°2'N 99°16'W	11.3	8.5	4.3			
19°8'N 99°42'W	11	6.2				
19°18'N 99°17'W	9.1	9				
19°20'N 98°35'W	9.5	8.5				
19°22'N 99°16'W	9	6.5				
19°23'N 99°11'W	11.5	7.2	8.4			
19°25'N 99°10'W	9.2	7.7	6.2			
19°25'N 99°10'W	9.2	7.2	6.5	4.8	4.7	6.5	8.4
19°27'N 99°10'W	11.5	5.1	6.3	8.5		
19°32'N 97°9'W	8.8	6.5				
19°42'N 101°16'W	11.5	8.8				
19°41'N 98°52'W	8.7	6.8				
19°43'N 99°13'W	10.3	6.2				
20°7'N 98°44'W	9.3	4.8				
20°10'N 102°53'W	10	10.8				
20°19'N 98°20'W	8.2	3.5	6.3			
20°52'N 100°56'W	6.8	7	6.7			
21°13'N 101°43'W	9	8.5				
21°57'N 102°17'W	7.7	6.3				
23°22'N 105°32'W	6.6	3	4.5			
24°2'N 104°54'W	6.8	3.2	3.8			
24°11'N 105°2'W	8.8	4.5				
24°47'N 101°31'W	8.1	5				
28°24'N 107°26'W	6.5	3.8				

habitats is almost as great as all habitats put together. Indeed, the area in the vicinity of Mexico City (19°-21° North; 2200-2600 meters high) includes males that range from 0.38 to 0.99 of the female's size; all localities, including the dry desert land in Sonora, have males of only marginally greater range -- 0.38 to 1.08 of the female's size.

DISCUSSION

Many hypotheses have been advanced to explain male dwarfism. FABER (1994) reports that some male jumping spiders in the species *Zygoballus rufipes* mature at an earlier instar, in an attempt to avoid competition with larger males that mature later in the season. The theory of evolution of senescence also explains male dwarfism. It

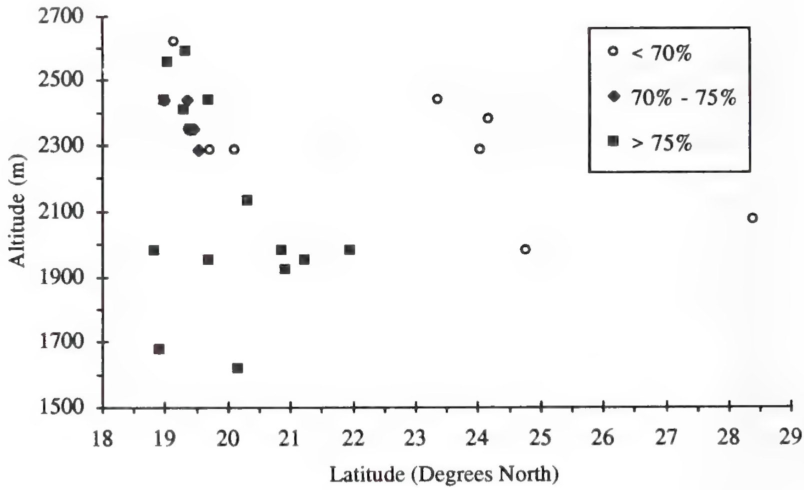

FIG. 3

Metepeira spinipes. Percent male size relative to average female size for each locality, plotted against altitude and latitude.

predicts that males that suffer higher mortality rates should undergo more rapid senescence following maturation (WILLIAMS 1957). A restricted adult life-span would increase selection for a shorter maturation time, thus leading to dwarfism.

The results of this study are consistent with the observation that sexual size dimorphism is greater under conditions of high male mortality (VOLLRATH & PARKER 1992) and suggest that variability in sexual dimorphism is a response to variability in communal behavior across lush and harsh environments. Males that live with females in large colonies, as in the case of *M. incrassata*, are unlikely to suffer relatively heavy losses due to predation and accidental death. Males that are forced to travel large distances in search of widely dispersed females, such as species A, will suffer far greater losses than their sedentary siblings. Consequently, one observes a higher degree of sexual size dimorphism in species A than in *M. incrassata* (Fig. 2).

VOLLRATH & PARKER (1992) further argue that higher adult male mortality reduces male intrasexual competition and thereby attenuates the competitive advantage of larger size. Males thus relieved of strong selection for larger size can decrease their chances of juvenile mortality by maturing earlier and undergoing fewer molts, thereby leading to dwarfism (VOLLRATH & PARKER 1992). On the other hand, MAIN (1990) argues that small male mygalomorph spiders are better designed to avoid hazards, such as drought or starvation, and thus would be favored in harsh environments with well dispersed females. Larger males may be more susceptible to predators and less efficient at traveling over land (Bristowe, 1941). Perhaps smaller males are better able to pull themselves along fine airborne threads when passing from one shrub to another.

If the operational adult sex ratio for a given habitat is the primary cause of selection for male size, then one might expect average habitats, hosting semi-communal populations with less skewed sex ratios, to produce males of intermediate dimorphism. Because *M. spinipes* is distributed across a wide range of habitats, this hypothesis was tested. In fact, these average habitats have a wide range of different size males (Fig. 3), suggesting that variation in male size could be the result of two specific and separate strategies: large males competing with other males in colonies; and dwarf males, adapted for cross-country travel, searching for solitary females.

Nonetheless, these results are not inconsistent with the approach of Vollrath and Parker, and it is likely that male dwarfism is in fact a combination of reduced intrasexual competition and specialization for locating dispersed females in harsh environments.

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Salticidae (Araneae) distribution over Indonesian and Pacific Islands

Jerzy PRÓSZYŃSKI
Muzeum i Instytut Zoologii PAN, ul. Wilcza 64, 00-679 Warszawa, Poland.

Salticidae (Araneae) distribution over Indonesian and Pacific Islands. - Indonesian and the Pacific Islands is a classical area for biogeographic considerations. Unfortunately the taxonomy of Salticidae from that area is poorly known. Preliminary results of three rich collections indicate that the majority of Polynesian and Micronesian genera is not isolated from those of Indonesian islands, so we can speak of "island genera". Out of 87 island genera examined, 72% have representatives on Asian mainland (some also on Australia), in contrast to 15% having only Australian or New Guinean representatives. About 13% of genera are limited to islands, without relatives on either continent, as far as known. A striking aspect of the island Salticidae fauna is an extensive island type speciation on archipelagoes of smaller islands and a continental type on larger islands. There are no endemic genera on small islands.

Key-words: Araneae – biogeography – Indonesia – Micronesia –Polynesia – Pacific – Salticidae – spiders.

INTRODUCTION

Many opinions have been expressed about the spider fauna of islands: Berland 1934, Lehtinen 1980, Zabka 1988, 1990, 1993, 1994. To draw conclusions unbiased by previous views, I had access to collection of exceptional value, far more complete and rich than those available to the previous authors. The most important collections I studied were: J.W. Berry - J. Beatty collection from Pacific Islands, Ch. Deeleman-Reinhold collection from SE Asia and a collection of ant-like Salticidae from Malaysia, constituted by M. Edmunds. Taxonomic descriptions of species from the Pacific Island were prepared and deposited for press (Berry *et al.*, in press, a, b, and in preparation); the Indonesian and SE Asian collections were sorted out and the species will be described in due time.

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RESULTS AND DISCUSSION

The study of island fauna is full of surprises. Seemingly widespread species in some genera appear, when carefully examined, to present dozens (possibly even more) of closely related distinct species. It just seems that every small island has a species of ist own, due to allopatric — island speciation. This calls for a special attention: after identification of the genus one has to search for specific differences in similarly looking specimens from every island.

Other genera, however, appear so differentiated that their relationships become clear only after a detailed analysis. This may be due to the continental type speciation, taking place on larger islands, as Viti Levu, not to mention even that on real continents. A good example of such an advanced differentiation is provided by the genus *Sobasina* (for description see Berry et al., in preparation).

The distribution of genera shows their geographical provenance and relationships with faunas of other areas (see enclosed table). There are only few endemic genera, those mentioned up to now turned out to be misidentifications. The Salticidae faunas of Polynesia, Micronesia and Indonesia seem to have clearly Oriental relationships, some of their genera occurring also in such distant areas as the Palaearctic Far East, Central Asia, the Mediterranean and Africa. My analysis does not include New Guinea, Melanesia, New Zealand and Hawaii, the characteristics of these faunas are unknown to me. On the other hand, a number of Oriental genera also reaches Australia and are of zoogeographical significance.

TABLE 1

Distribution of Salticidae genera on South Pacific and Indonesian islands

Abbreviations: Af – Africa, Au – Australia, Fj – Fiji, Me – Melanesia, Mi – Micronesia, Mo – Moluccas + Sulawesi, NG – New Guinea, NZ – New Zealand, OM – Oriental mainland, Pal – Palaearctic; Po – remaining Polynesia, Sa – Samoa and Tonga, SG – Greater Sunda Is., SL – Lesser Sunda Is., Ta – Tahiti, citrop – circumtropical. Occurrence of genera: + – catalogue data (PRÓSZYŃSKI 1995), x – occurrence confirmed on studied collection, X – genus previously unknown from the island.

Genus	Au	NG	NZ	Me	Ta	Sa	Fj	Po	Mi	Mo	SL	SG	OM	Af	Pal	other
Omoedus	+	+					X			+						
Trite	+		+	+		+		x	x							
Zenodorus	+	+		+			X	+	X	+						
Palpelius	+	+		+		X		X	+		+					
Ascyltus	+	+		+		+		x		+		x				Hawaii
Holoplatys	+		+	+					X			+				
Ergane	+								x			x				
Servaea	+											x				
Damoetas	+										X	X				
Ptocasius	+											+	x			
Mintonia	+											x	+			
Bathippus	+	x								+		x	x			
Bavia	+	x			x		x	x	x	x		x	x			
Rhene	+	+					+			x		x	+	+	+	Hawaii
Cytaea	x	x					x	x	x	x	x	x	+			

Genus	Au	NG	NZ	Me	Ta	Sa	Fj	Po	Mi	Mo	SL	SG	OM	Af	Pal	other
Euryatus	+	+							+	x	X	X	X			
Plotius	+	+								+	x	x	+			
Diolenius	+	+								x		x	x			
Hasarius	+	+			+		x	x	x	+	x	+	x	+	+	citrop
Menemerus	+	x					x	x	x			x	x	+	+	citrop
Plexippus	+	+					x	x	x	+	X	x	x	x	x	citrop
Bianor	+						X		X		X	x	+	+	+	
Euophrys	x						X		X			X	+	+	+	
Myrmarachne	+						X	+	X	X	x	x	x	+	+	
Pseudicius	+						X	x	x			x	x	+	+	
Evarcha	+							+	X		x	x	x	+	+	
Thyene	+										x	X	+	+	+	
Harmochirus	+										X		+	+	+	
Hyllus	+									+	x	x	x	+		
Cosmophasis		+					X		x	x	x	+	x	+		
Cocalodes		+						+		+		x				
Thorelliola		+						x	X	x		+				
Thiania		+								+	X	x	x			Hawaii
Telamonia		+								+	x	x	x	+	+	
Poecilorchestes		+										X				
Donoessus		X										x	X			
Chalcolecta		+											+			
Furculattus		x														
Sobasina				+			X	X	X	X			X			
Athamas				+	x	x		x	X	X						
Efate				+			X	x	X							
Modunda						Marquesas								+		Hawaii
Flacillula						+		x	X			+				
Gen.n. [I]							X									
Gen.n. [B]							X									
Artabrus									+		X	x				
Ligurra									X		X	+	X			
Phintella									X	X	x	X	X		+	
Carrhotus										+	X	x	x		+	
Epeus										X	X	x	x		+	
Epocilla										+		x	x		+	Hawaii
Siler										X	X	+	x		+	
Marengo										X	X	X	X	+		
Agorius										x	x	x	x			
Pristobaeus										x	X	X	X			
Viciria										+	X	+	+			
Spartaeus										+	X	+	x			
Orthrus										X		x	X			
Gelotia										+		x	+			
Pystira										+		x	+			
Stertinius										+		x				
Brettus										x		+				
Mantisatta										X	+					
Burmattus											X		+		+	
Asemonea											x	x	+	+		
Belippo											X	X	X	+		
Gedea											X	X	x			
Stergusa											X	X	+			
Onomastus											X	x	x			

Genus	Au	NG	NZ	Me	Ta	Sa	Fj	Po	Mi	Mo	SL	SG	OM	Af	Pal	other
Phaeacius											X	+	+			
Microhasarius											X	+				
Maileus											x					
Phlegra												X	+	+	+	
Plexippoides												X	+		+	
Synagelides												X	x		+	
Langona												X	x	+	+	
Taraxella												x	+			
Mantius												+	x			
Emathis												x	+			
Curubis												X				
Irura												X	+			
Laufeia												x	+			
Nanneus												X	+			
Orisania												X	+			
Orisima												x	+			
Panysinus												x	+			
Pancorius												x	+			

TABLE 2

Number of genera of Salticidae distributed on Pacific Islands
(a sample of 28 genera, cosmopolitic ones not included)

Car = Caroline, Coo = Cook, Fij = Fiji, Mar = Marshall, Maq = Marquises, Gil = Gilbert, NHb = NHebrid + NCaledonia, Pal = Palau, Sal = Salomons, Sam = Samoa, Soc = Society, Ton = Tonga, Tua = Tuamotu, Tub = Tubuai, x- occurrence

	Pal	Car	Mar	Gil	Fij	Ton	Sam	Coo	Soc	Tua	Tb	Maq	Sal	NHb
Penionomus				x										
Phintella		x												
Zenodorus		x			x									
Thorelliola		x	x				x		x			x		
Flacillula		x						x						
Trite		x						x			x			x
Bavia	x	x		x			x	x			x	x	x	
Efate	x	x	x		x									
Athamas	x	x					x			x				x
Sobasina	x				x	x								x
Pseudicius	x		x		x		x							
Cytaea	x				x		x							
Bianor	x				x									
Cosmophasis	x				x									
Euophrys	x				x									
Myrmarachne	x				x									
Palpelius	x													
Evarcha	x													
Holoplatys	x													
Ligurra	x													
Ergane	x													

	Pal	Car	Mar	Gil	Fij	Ton	Sam	Coo	Soc	Tua	Tb	Maq	Sal	NHb
Omoedus					x									
Gen n. (I)					x									
Gen n. (B)					x									
Ascyltus						x								x
Saitis														x
Pseudomaevia								x	x					
Modunda														x
	15	8	3	2	13	2	5	3	2	2	2	3	4	5
	Pal	Car	Mar	Gil	Fij	Ton	Sam	Coo	Soc	Tua	Tb	Maq	Sal	NHb

TABLE 3

Summary of distribution of 87 genera of Salticidae known from the South Pacific and Indonesian islands

Restricted to South Pacific Islands	4 = 5%
Restricted to South Pacific and Indonesia	7 = 8%
Reaching Asian mainland, but not Australia	38 = 44%
Reaching both Asian mainland and Australia	16 = 18%
Reaching Australia/New Guinea, but not Asian mainland	13 = 15%
Cosmopolite or widely distributed	9 = 10%

In general, the number of genera occurring on a particular group of islands decreases with increasing distance from the Oriental mainland, as summarized below:

> Greater Sunda = 73; Lesser Sunda = 43; Molucas = 34; the whole Micronesia = 22 (Palau = 15, other Carolines = 7, Gilbert = 2, Marshall = 3); the whole of Polynesia = 21 (Fiji Is. = 13, Tonga = 2, Samoa Is. = 5, Cook Is. = 3, Society Is. = 2, Tuamotu Is. = 2, Tubuai Is. = 2, Marquesas = 3). The data for Melanesia = 6; (Salomon Is. = 1, New Hebrides and New Caledonia = 5) are incomplete and shall not be considered further.

That decrease accords with the classical, textbook correlation between distance, area and number of species, as expressed in the island biogeography model (MACARTHUR & WILSON 1967). However, the detailed distribution patterns do not confirm this general rule. It seems that dispersal from one group of islands to another was not gradual, but occurred in jumps. Genera were settling on one group of islands, omitted the adjacent islands and colonized some more distant islands instead. Human influences might be responsible for it. Dispersal of species within group of islands, however, is rather gradual.

I am unable yet to comment upon the Salticidae fauna of Hawaii in detail. Its striking feature is, however, the occurrence of Oriental (*Epocilla*, *Rhene*, *Thiania*) and North American (*Phidippus*) genera, not known from Micronesia and Polynesia.

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Consequences of pesticide use on spider communities in mango orchards

Donna RAYNER, Michael COATES & Robert NEWBY
Department of Biology, Central Queensland University,
Rockhampton, Queensland 4702, Australia.

Consequences of pesticide use on spider communities in mango orchards. - A preliminary study was performed during spring/summer 1993 to determine the effects of pesticide use on spider communities in Central Queensland mango orchards. The results suggest that the frequent use of pesticides reduced abundance, species richness and species diversity of spiders in these orchards, while infrequent application of pesticides did not appear to result in a change in these properties. However, when relative species abundances in orchards which have had frequent, infrequent and no pesticide applications (n = 3, n = 6 & n = 3, respectively), over three sampling periods, were compared by non-parametric multivariate analysis, changes in community structure were indicated. Web-building and hunting spiders were both found to be vulnerable to pesticides.

Key-words: Pesticides - spider abundance - species richness - species diversity - relative species abundance.

INTRODUCTION

In many field crops and orchards, pesticides are extensively used to control pests and diseases. One of the main concerns for growers is the increasing cost of pesticides and the risk of insects becoming resistant to the pesticides used. Thus, interest in the use of natural predators in agroecosystems is increasing. In recent years emphasis has been placed on the action of spiders as biocontrollers within these systems. Spiders are ubiquitous and totally predacious making them an obvious possibility as biocontrol agents. RIECHERT & LOCKLEY (1984) suggest that it is the spider community as a whole which is the stabilising influence on pest species in agroecosystems. The maintenance of community diversity as well as abundance of spiders is required to maximise the probability of a range of pest species being predated (RIECHERT & LOCKLEY 1984).

Agroecosystems tend to have unstable communities due to the use of pesticides, tilling of the soil and removal of the crop during harvesting. All of these facts may

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disrupt the community structure of spiders. Orchards are established agroecosystems where the trees are maintained for several years. Therefore, structural disruption is less than in other types of agroecosystems making them an appropriate situation in which to study the disruptive influences of pesticides on spider communities.

Mangoes are a commonly grown fruit in Central Queensland. The annual production of fruit is valued at approximately 2 x 10^6 Australian dollars per year. Many orchardists use pesticides to control pest species which are prevalent in the area. This study is a preliminary assessment of the effects of pesticides on abundance, species richness, species diversity and community structure of spiders within mango orchards.

MATERIAL AND METHODS

The mango orchards used in these studies were relatively small, ranging in size from 30 to 200 trees. They were all established orchards, with fruit bearing trees at least three years of age, and were all located in coastal areas in Central Queensland. Twelve orchards were chosen and separated into three types according to the amount of pesticide used during the three month sampling period. Unsprayed orchards received no pesticides (copper oxychloride and mancozeb). The infrequently sprayed orchards received heavy applications of fungicides but minimal insecticides (methidithion, endosulphan and dimethoate), and the frequently sprayed orchards received heavy applications of both fungicides and insecticides.

Spiders were collected over a 30 minute period from the foliage of 2 trees in each orchard during spring/summer (October, November and December), 1993. The data from the two trees were combined to give a single one hour sample per orchard for each of the three sampling times. Wherever possible the spiders were identified to species or genus level. Individuals which were unable to be identified (mainly immature) were allocated an identification number.

Species were classified as belonging to one of two guilds. Those individuals which required the use of a web for capturing prey were placed in the web-building guild. This included the clepto-parasite *Argyrodes antipodianus* which occupied the webs of larger web-building spiders and foraged for small prey trapped in the web. The hunting guild included those spiders which search for prey and did not require a web to capture prey.

The abundance and species richness of spiders were determined for each orchard at each sampling time. Species diversity within each orchard was assessed by the Shannon-Wiener Diversity Index (KREBS 1972).

The effects of pesticides on the relative abundance of spider species, or community structure, was assessed through the use of a non-parametric multivariate analysis. The ANOSIM program (CLARKE 1993) was used to test the null hypothesis that there was no difference in the relative abundance of species between the frequently, infrequently and un-sprayed orchards. This test compared the abundance of each of the spider species present in each orchard at each sampling time. The Bray-Curtis index was used to produce a matrix consisting of the similarities between each pair of orchards. The average difference between the similarities within and between

groups (eg. frequently sprayed compared to unsprayed) were then determined to give a true R value. The labels of the orchards were then randomly permutated (1000 times in this case) and a test R value was calculated for each permutation. If the proportion of test R values greater than the true R was less than 0.05 the null hypothesis was rejected.

RESULTS

A comparative list of the spider species and the total number of individuals of each species found in unsprayed and frequently sprayed orchards are shown in Table I. Mean spider abundance, species richness and Shannon-Wiener Diversity Indices for each sampling period in each type of orchard are shown in Figures 1, 2 & 3, respectively. The mean values for each parameter were less for frequently sprayed compared to unsprayed and infrequently sprayed orchards. Infrequently sprayed and unsprayed orchards appeared similar.

The structure of the communities in frequently, infrequently and un-sprayed orchards was examined with a one-way ANOSIM test (CLARKE 1993), treating the samples from October, November and December as independent relicates. The infrequently sprayed orchards were found to be significantly different from infrequently sprayed and unsprayed orchards ($P = 0.002$ in both cases). The community structure of unsprayed and infrequently sprayed orchards were also found to be significantly different ($P = 0.017$). Only *Badumna* sp. and *Scytodes fusca* had an increase in the abundance of more than two individuals. *Badumna* sp. increased by one or two from 19 to 66 individuals after pesticides were used. *Poltys* sp. and *Nephila* sp. increased by one or two in the individuals in unsprayed compared to frequently sprayed orchards. *Psuedohostus squamous* had 1 individual in each of the unsprayed and frequently sprayed orchards. The remaining 39 species of the 43 species decreased in abundance (Table 1).

The total abundances of web-building and hunting spiders for each type of orchard in each sampling period are shown in Figure 4. Web-building spiders were more abundant than hunting spiders in all three types of orchard. The number of both web-building and hunting spiders appeared to be reduced by the use of pesticides.

DISCUSSION

These preliminary results suggest that spiders are greatly affected by the frequent use of pesticides in mango orchards. Not only was the abundance of spiders reduced but, species richness and diversity were also reduced. The decrease in the number of spider species and their abundance reduces the effectiveness of these predators in controlling pest species. RIECHERT & LOCKLEY (1984) suggested that no one species, no matter how abundant, is capable of holding pests in check. Therefore, community diversity must be maintained to maximise the number of different predators that will encounter a range of pest species.

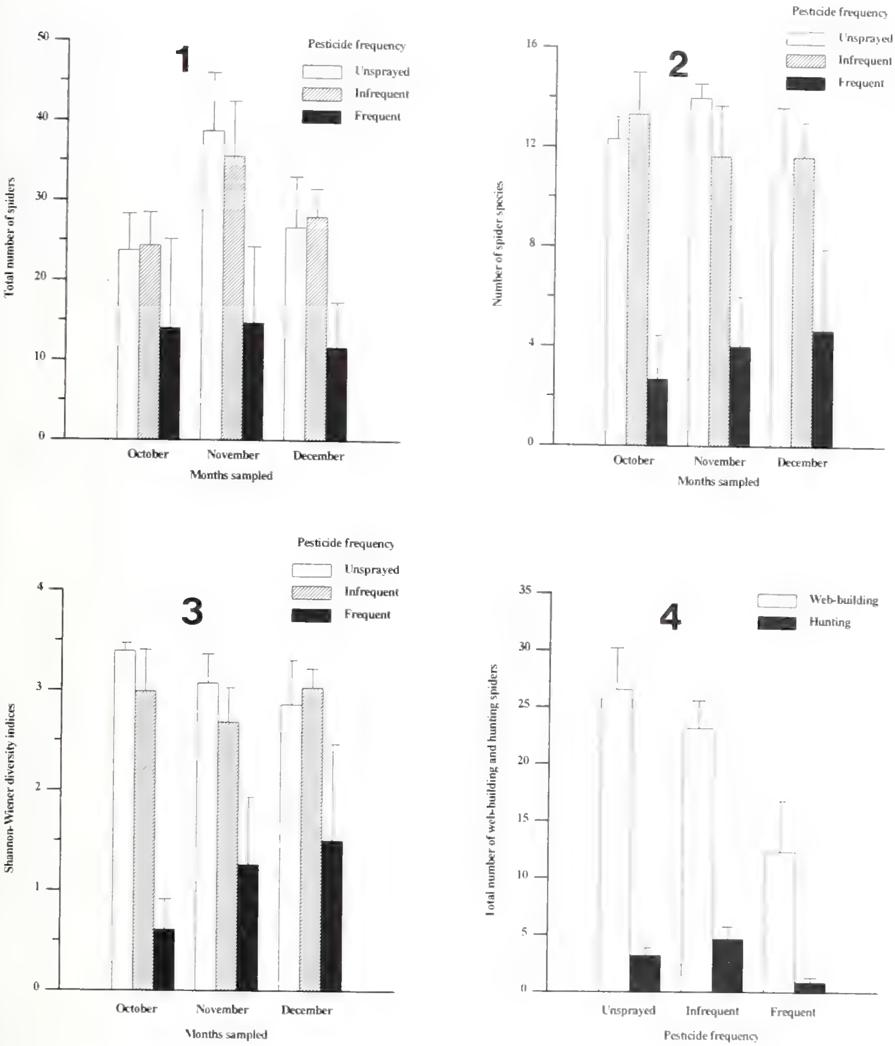
The infrequent use of pesticides did not appear to have the same disruptive effect as the more frequent use of pesticides. RIECHERT & LOCKLEY (1984) suggested that by limiting the amount and frequency of pesticides used in agroecosystems, spider

TABLE I

List of spider species with total number of individuals found in unsprayed and frequently sprayed mango orchards in Central Queensland during October, November and December, 1993.

Family	Species	Total no. of individuals unsprayed	Total no. of individuals frequently sprayed
F. Araneidae	* *Zealaranea* sp.	55	1
F. Araneidae	* *Argiope* sp.	17	16
F. Araneidae	* *Cyclosa* sp.	11	0
F. Araneidae	* *Cyrtophora exanthematica*	10	3
F. Araneidae	* *Cyrtophora hirta*	10	3
F. Araneidae	*Cyclosa* sp.	6	0
F. Araneidae	*Araneus praesignus*	5	2
F. Araneidae	*Poltys* sp.	3	4
F. Araneidae	*Nephila* sp.	1	3
F. Araneidae	*Cyclosa* sp.	3	0
F. Araneidae	*Gasteracanthus* sp.	3	0
F. Araneidae	*Nephila maculata*	3	0
F. Araneidae	unidentified immature	2	0
F. Araneidae	*Gasteracanthus taeniata*	1	0
F. Araneidae	unidentified immature	1	0
F. Clubionidae	*Cheiracanthium* sp.	3	0
F. Clubionidae	*Cheiracanthium* sp.	2	0
F. Desidae	*Badumma* sp.	19	66
F. Oxyopidae	*Oxyopes maculensis*	3	2
F. Oxyopidae	*Psuedohastus squamous*	1	1
F. Salticidae	*Cytaea* sp.	4	0
F. Salticidae	unidentified immature	3	0
F. Salticidae	*Cosmophasis bitaeniata*	2	0
F. Salticidae	unidentified immature	2	0
F. Salticidae	unidentified immature	1	0
F. Salticidae	unidentified immature	1	0
F. Salticidae	unidentified immature	1	0
F. Salticidae	unidentified immature	1	0
F. Salticidae	unidentified immature	1	0
F. Scytodidae	*Scytodes fusca*	0	3
F. Tetragnathidae	*Leucauge* sp.	2	0
F. Tetragnathidae	unidentified immature	1	0
F. Theridiidae	* unidentified immature	9	2
F. Theridiidae	* *Argyrodes antipodianus*	7	0
F. Theridiidae	*Archearania mundula*	5	1
F. Theridiidae	unidentified immature	4	0
F. Thomisidae	*Dianea* sp.	1	0
F. Thomisidae	*Xysticas* sp.	1	0
F. Thomisidae	unidentified immature	1	0
unidentified	immature	4	0
unidentified	immature	3	0
unidentified	immature	2	0
unidentified	immature	1	0

* large decreases in spider abundance when comparing unsprayed with frequently sprayed orchards.



FIGS 1–4

Fig. 1: The mean and standard errors of spider abundance in frequent, infrequently and frequently sprayed (n = 3, n = 6 & n = 3, respectively) mango orchards during spring/summer 1993 in Central Queensland. Fig. 2: The mean and standard errors of number of species in frequent, infrequently and frequently sprayed orchard (n = 3, n = 6 & n = 3, respectively) mango orchards during spring/summer 1993 in Central Queensland. Fig. 3: The mean and standard errors of Shannon-wiener diversity indices for frequently, infrequently and un-sprayed (n = 3, n = 6 & n = 3, respectively) mango orchards during spring/summer 1993 in Central Queensland. Fig. 4: The mean and standard errors of abundance of web-building and hunting spiders in frequent, infrequent and un-sprayed (n = 3, n = 6 & n = 3, respectively) mango orchards during spring/summer 1993 in Central Queensland.

numbers and diversity may be conserved. The results from this study suggest that infrequent use may indeed maintain spider numbers and diversity. However, the relative abundance of spider species (community structure) appears to have been disrupted in orchards with infrequent as well as frequent pesticide use. This suggests that some spider species are more susceptible to pesticides than others. When the abundance of each species was compared for unsprayed and frequently sprayed orchards a similar result was observed. Out of the 44 species collected, 38 species decreased in abundance suggesting susceptibility to the pesticides. The largest decreases were found for the (species marked), whereas *Badumna* sp. was the only spider which showed a significant increase in numbers (Table 1). If those spiders which are most susceptible to pesticides are also the most effective predators of pest species then even the infrequent use of pesticides will diminish biocontrol. The results of this study suggest that the relationship between effective predation of pest species and susceptibility to pesticides needs to be investigated for such naturally occurring biocontrollers.

Both web-building and hunting spiders appeared to be susceptible to the frequent use of pesticides. This result conflicts with the generally accepted conception, that web-building spiders are more susceptible to pesticides because they are directly exposed to the fumigation process as webs tend to collect agrochemical sprays (Samu *et al.* 1992). Hunting spiders are more likely to avoid the pesticides as webs are not used and due to their behaviour of hiding.

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Study of a narrow hybrid zone between two wolf spiders, *Lycosa ammophila* and *Lycosa ericeticola*, in north Florida (Araneae, Lycosidae)

Jonathan REISKIND & Paula E. CUSHING
Department of Zoology, University of Florida, Gainesville, FL 32611, USA.

Study of a narrow hybrid zone between two wolf spiders, *Lycosa ammophila* and *Lycosa ericeticola*, in north Florida (Araneae, Lycosidae). - The Rosemary Wolf Spider, *Lycosa ericeticola* Wallace, is a member of the *lenta* group of *Lycosa* with a distribution restricted to approximately 3000 hectares. It is parapatric to the widely distributed Sand Loving Wolf Spider, *Lycosa ammophila* Wallace. The genitalia of the males of the two species are dramatically distinct. The two species come into contact in an area of habitat typical for both species and form a narrow hybrid zone of less than 300 meters in width. A morphological study across this overlap zone documents intermediates in male genitalic structure and size dimensions. Behavioral studies demonstrate that the two species readily court and copulate in captivity. Probable historical, ecological and behavioral causes of the speciation of the two species and their subsequent hybridization are discussed.

Key-words: Araneae - Lycosidae - Hybrids - *Lycosa* - Florida - Morphology - Behavior.

INTRODUCTION

Two closely related wolf spiders, the Sand Loving Wolf Spider, *Lycosa ammophila* Wallace, and the Rosemary Wolf Spider, *Lycosa ericeticola* Wallace, have similar habitat preferences but differ in their geographic distributions (Wallace 1942). Both are members of the *Lycosa lenta* group. They inhabit sandhill and high pine habitats (Myers 1990) and are nocturnal hunters in open sandy areas. *L. ammophila* is widespread across northern Florida with a range of more than 5,000,000 hectares whereas *L. ericeticola*, which has been designated a threatened species (Franz 1982), has a highly restricted range of about 3000 hectares, and is restricted to areas with high concentrations of the Florida rosemary, *Ceratiola ericoides*. The distributions of the two species are parapatric (Fig. 1), the western boundary of *L.*

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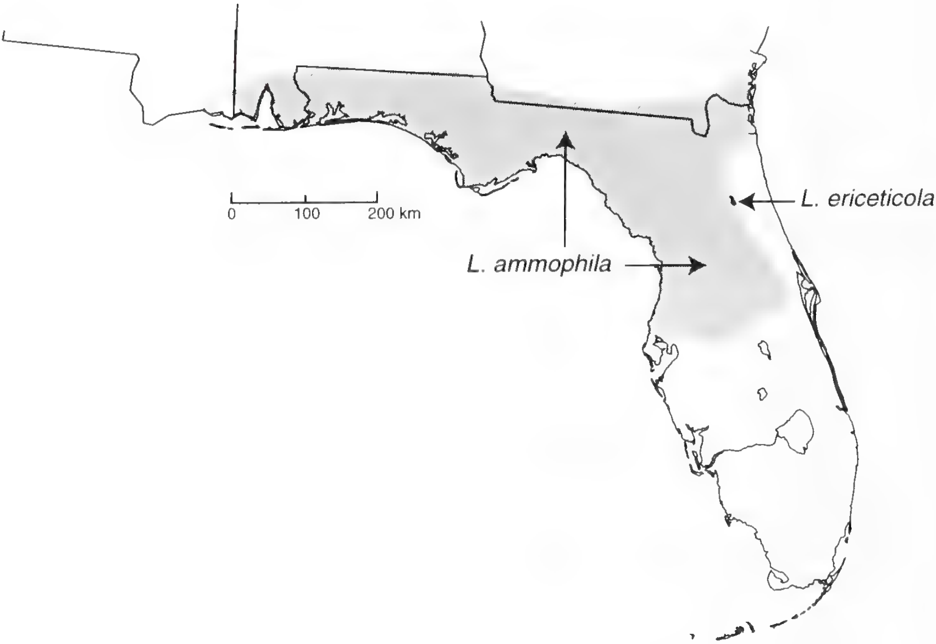


Fig. 1

Distribution map of *Lycosa ammophila* and *L. ericeticola* in Florida (from WALLACE 1942, REISKIND 1987).

ericeticola abutting that of *L. ammophila* (REISKIND 1987). The habitat did not seem to be the limiting factor of its northern and western distribution. Rather, *L. ammophila* replaced *L. ericeticola* in those areas. In one such continuous habitat 6 km west of Interlachen, Florida (Fig. 2) (an area of mostly dirt roads and little development) both species were found together over an east-west distance of about 150 m.

The morphological variation in the male palps of these species is of special interest. Pedipalps of male spiders are used to transfer sperm to the female. They are key taxonomic characters and are diagnostic of specific distinctions in most higher spider groups. Probably the result of sexual selection by female choice (EBERHARD 1985), their detailed and often complex structure are consistent and stable within a species and almost invariably differ from closely related species. This is surely the case in these two species. In *L. ammophila* the median apophysis is straight with a chisel-like posterior medial retrorse tooth (Figs. 3 & 7) whereas in *L. ericeticola* the retrorse tooth is curved with its posterior ending in a distinct downward point (Figs. 4 & 8). A hand lens in the field allows easy discrimination of live specimens. There is no discernible genitalic variation within *L. ericeticola* or in the eastern populations of *L. ammophila* (WALLACE 1942).

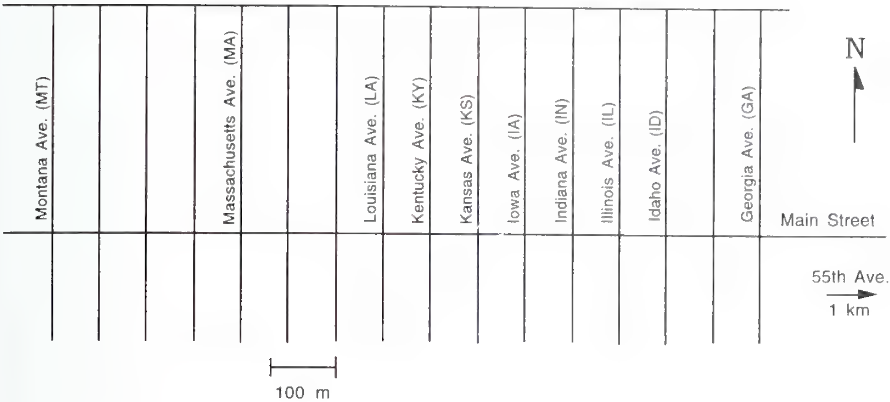


Fig. 2

Map of overlap region between *L. ammophila* and *L. ericeticola*. Collections were made within 100 m of Main Street at the cross streets named.

This paper will examine the two species in their area of overlap to determine if there is evidence for hybridization. Morphology, especially of the male genitalia, supplemented by a study of the effectiveness of their prezygotic isolating mechanisms will be used to test the hypothesis that *L. ericeticola* and *L. ammophila* hybridize.

METHODS

Ninety-five male spiders were collected along a transect crossing the overlap area. The transect was 2.8 km in length and spiders were collected up to 100 meters on either side of a central axis (Main Street in Fig. 2). The most concentrated collections were made in the area of sympatry.

Five measurements were made on each specimen. Three body dimensions: the length of the fourth leg, the carapace length and the carapace width, were made using calipers and are precise to within 0.1 mm. Two genitalic measurements were made by drawing the median apophysis of the male palp (viewed ventrally) using a camera lucida attachment to a Wild stereoscopic dissecting microscope. Measurements of the maximum length of the median apophysis (from the anterior end of its fulcrum to the posterior tip of the retrorse tooth) and its "depth" (see Fig. 5) were made from the drawings and are precise to within 0.001 mm. In addition the "depth"/length (D/L) ratio of the median apophysis was calculated.

All specimens were identified as either *L. ammophila* or *L. ericeticola* on the basis of clear qualitative genitalic features. Those specimens whose designation, based solely on the shape of the median apophysis, were uncertain (Figure 6) were labeled "intermediate" regardless of where they were found in the geographical distribution.

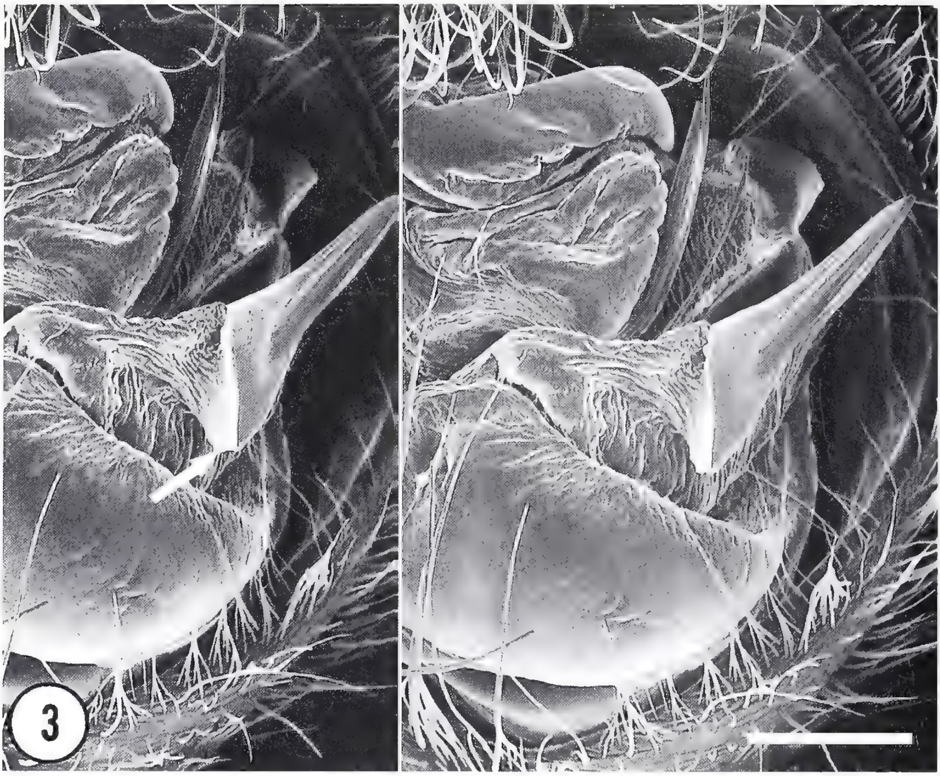


FIG. 3

A stereo ventral view of the left palp of *Lycosa ammophila*. Arrow points to retrorse tooth of the median apophysis. Scale line = 0.4 mm

The five morphological measurements and the D/L ratios allowed statistical comparisons of the two species and their "intermediates." In addition, Neff & Smith (1979) demonstrated the usefulness of a principal component analysis (PCA) in investigating suspected hybrids. The PCA allowed a graphic summary of these data and an independent evaluation of whether the "intermediates" fall between the putative parent species (WILEY 1981).

Adults of both species were tested for compatibility of courtship and copulatory behavior. Test animals were collected from within each species range and at least 1 km from the area of contact. This ensured that the females were of the appropriate identified species. Within and between species encounters were performed in which a male and a female were introduced into a sand filled arena of either 0.5 m x 0.5 m or 0.25 m x 0.5 m and observed for a period of 15 minutes. Efforts were made to use virgin individuals by allowing penultimate specimens to mature in the laboratory. Ten trials of each combination were run. The occurrence of courtship and copulation was noted.

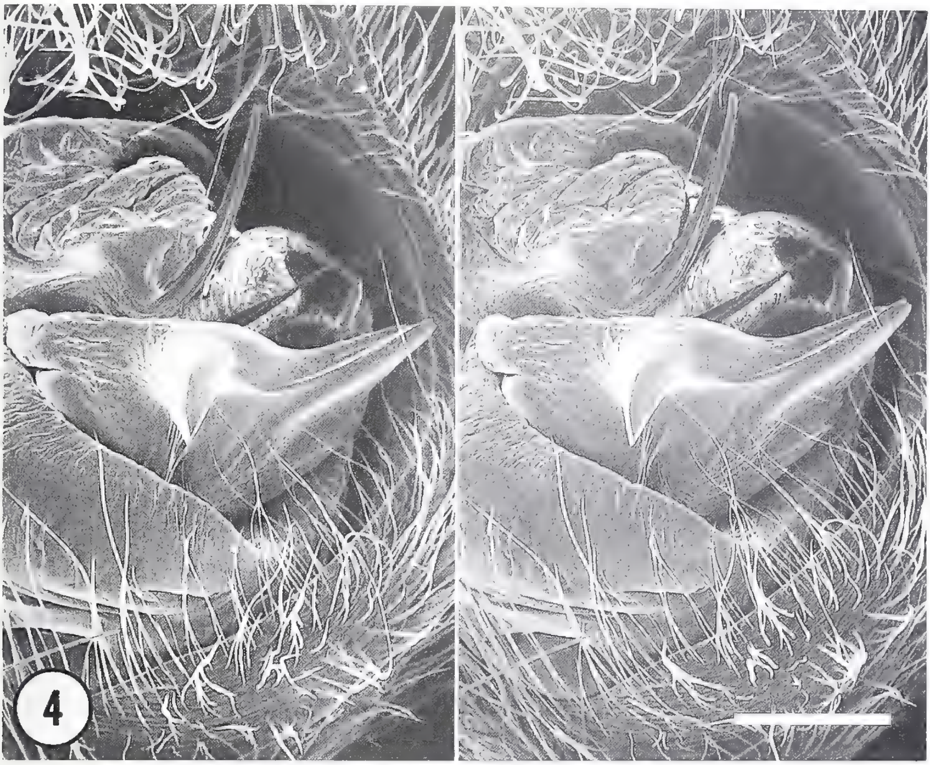


FIG. 4

A stereo ventral view of the left palp of *Lycosa ericeticola*. Scale line = 0.4 mm

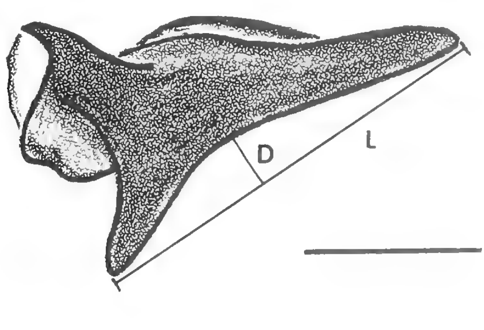


FIG. 5

The dimensions measured on the median apophysis of *Lycosa ericeticola*. L, length, D, depth. Scale line = 0.5 mm

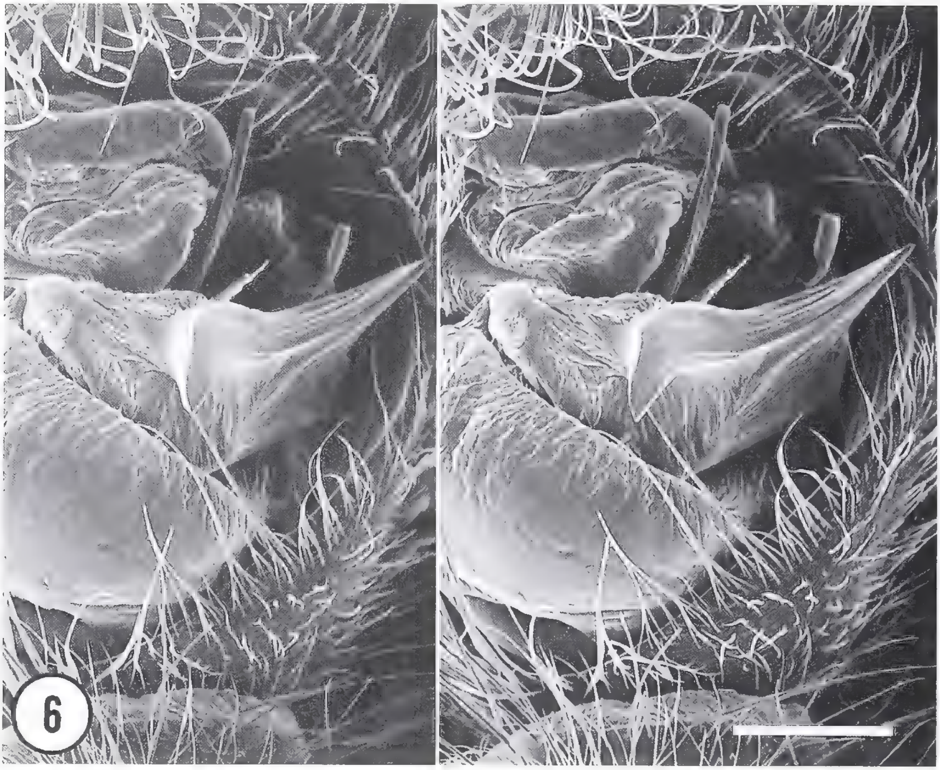


FIG. 6

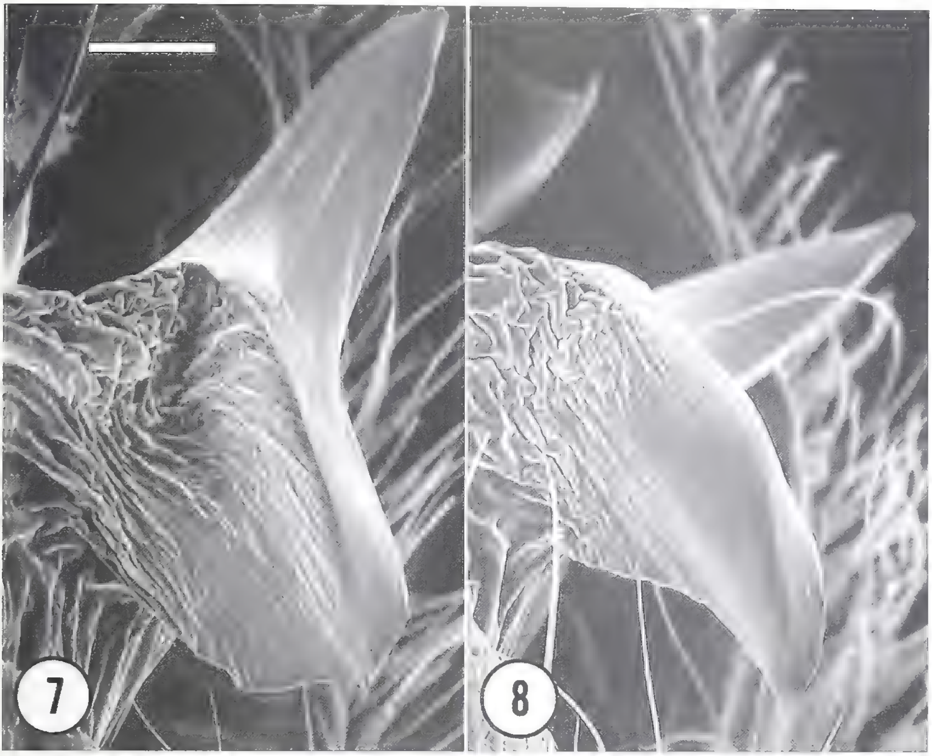
A stereo ventral view of the left palp of an "intermediate" male from Main St. and Kansas Ave. Scale line = 0.4 mm

RESULTS

Morphological intermediates were discovered along the transect in the narrow area where the two species come in contact. They were distributed over a distance of about 280 m, almost twice the width of the area in which both species were found together.

Figures 7-10 illustrate the proximal ends of the median apophyses of *L. ammophila*, *L. ericeticola*, and two "intermediates". The differences between the two species are qualitatively clear and dramatic. The "intermediates" are also distinct, perhaps examples of F_1 progeny.

The PCA allowed the reduction of the six parameters to two principal components accounting for over 87% of the total variance. The first PC (PC1) accounted for 62.8 % of the variance and the second (PC2) for 24.6%. Overall size differences appear to contribute most to PC1, while differences in median apophyses dimensions

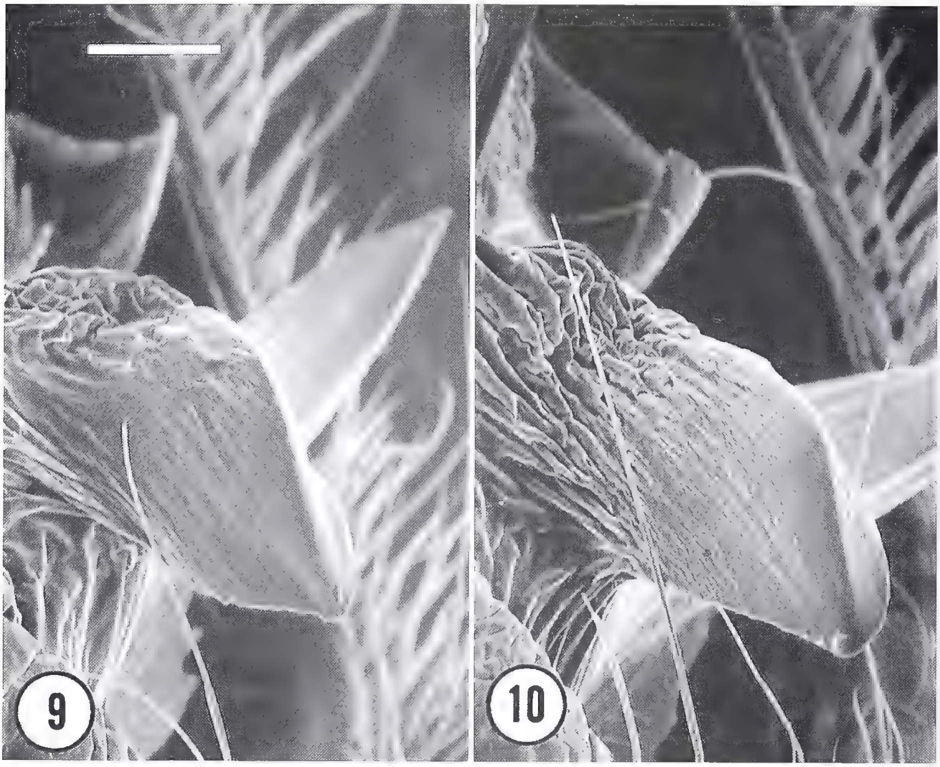


FIGS 7-8

Medial ventral view of the retrorse tooth of the median apophysis. 7. *L. ammophila*. 8. *L. ericeticola*. Scale line = 0.1 mm

primarily contribute to PC2. The resulting graph of these first two components (Fig. 11) allows a visual appreciation of the variation between the individuals of the three identifiable groups. Clearly the "intermediates" all fall between the two established species.

The qualitative differences of the genitalia are well reflected by the D/L ratios (Table 1). In areas where the two species were never caught together the D/L ratios of *L. ericeticola* range from 0.097 to 0.185 while those of *L. ammophila* range from 0.019 to 0.058 ($t=22.25$, $p<0.001$). In the area in which both species have been caught they are still distinct, *L. ericeticola* ranging from 0.084 to 0.179 and *L. ammophila* from 0.029 to 0.070. The "intermediate" genitalia have D/L ratios ranging from 0.055 to 0.111, bridging the gap between the two species. When comparing just those specimens of *L. ericeticola* found in the overlap area with the "intermediates" we found a significant difference in the mean D/L measurements ($t=3.31$, $0.001<p<0.01$). Likewise when comparing the *L. ammophila* specimens found in the overlap region with the "intermediates" ($t=7.38$, $p<0.001$).



FIGS 9-10

Medial ventral views of the retrorse tooth of the median apophysis of two "intermediate" specimens. Scale line = 0.1 mm

The change of D/L ratios along the transect clearly shows the narrow area (about 280 m) in which both species and "intermediates" are found (Fig. 12).

The results of the pairings are recorded in Table 2. The visible expression of male courtship in both species involves the male raising and vibrating his first legs followed by rubbing his first tarsi on the carapace of the female. If the female accepts the advances of the male she will allow him to copulate. A chi-square analysis (df= 2, chi-square= 0.472, $0.5<p<0.9$) indicates no significant difference within and between species with respect to courtship and successful copulatory behavior. From these results there appear to be no well established premating isolating mechanisms between these two species.

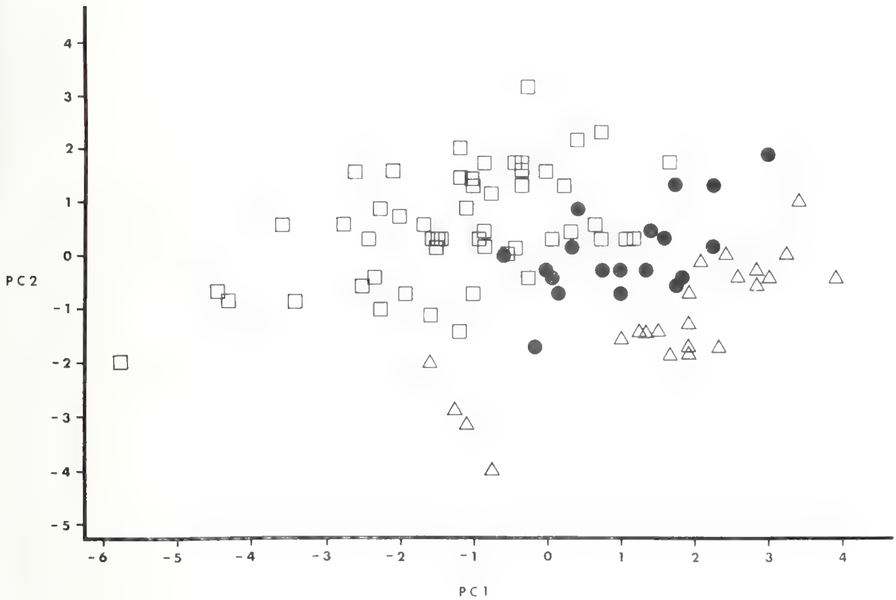


FIG. 11

First and second principal components of the PCA analysis. Open triangles = *L. ammophila*, open squares = *L. ericeticola*, solid circles = "intermediates."

TABLE 1

The D/L ratios of the three forms from different locations along the Main Street transect (see Fig. 2).

		Location										
		MT	MA	LA	KY	KS	IA	IN	IL	ID	GA	55th
L. ammophila	N=	3	6	4	5	6						
	mean:	0.041	0.033	0.041	0.045	0.044						
	max:	0.042	0.058	0.070	0.056	0.069						
	min:	0.039	0.019	0.029	0.033	0.029						
	S.D.:	0.002	0.015	0.020	0.009	0.014						
intermediates	N=			1	2	10	6					
	mean:			0.055	0.064	0.081	0.095					
	max:				0.064	0.104	0.111					
	min:				0.063	0.062	0.066					
	S.D.:				0.001	0.014	0.016					
L. ericeticola	N=				1	7	2	8	9	3	13	9
	mean:				0.102	0.109	0.143	0.127	0.139	0.138	0.151	0.149
	max:					0.142	0.179	0.179	0.185	0.158	0.174	0.171
	min:					0.084	0.107	0.106	0.097	0.119	0.124	0.124
	S.D.:					0.021	0.051	0.022	0.025	0.020	0.014	0.015

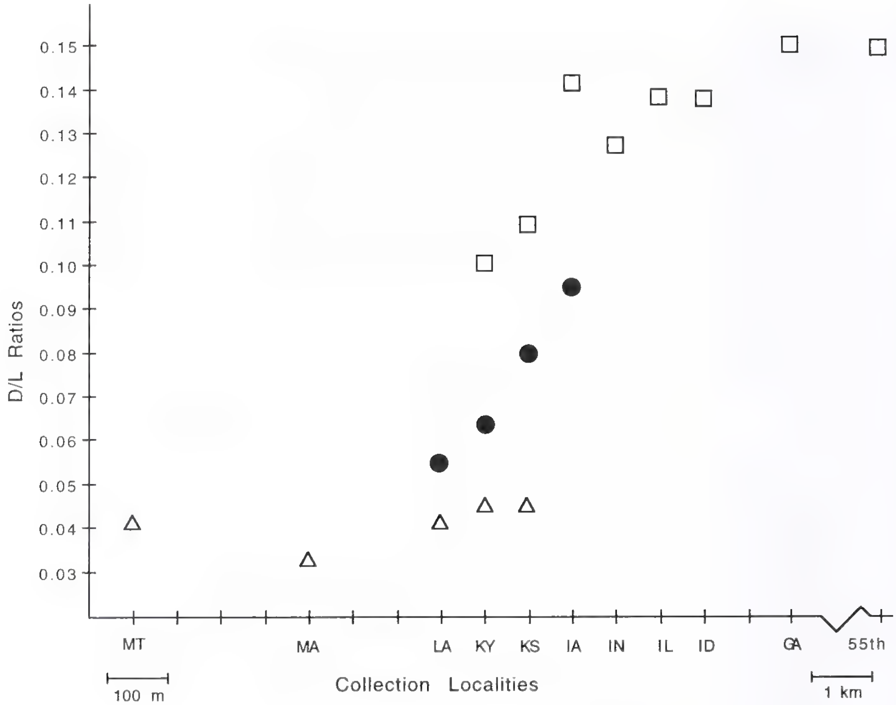


FIG. 12

D/L ratios. Open triangles = *L. ammophila*, open squares = *L. ericeticola*, solid circles = "intermediates." For locality abbreviations see Fig. 2.

TABLE 2

Results of pairing trials between and within the two species. L. ammophila and L. ericeticola

male	female	no male courtship	male courtship no copulation	copulation
L. ammophila	L. ammophila	5	1	4
L. ammophila	L. ericeticola	3	2	5
L. ericeticola	L. ammophila	7	1	2
L. ericeticola	L. ericeticola	3	2	5

DISCUSSION

All the evidence points to the presence of natural hybridization occurring between *L. ammophila* and *L. ericeticola* in an extremely narrow area where their distributions presently overlap. Morphological intermediates are found within and somewhat beyond this area. The statistically significant difference between each puta-

tive parent species and the "intermediates" suggests the production of F1 hybrids by interbreeding but suggests little if any introgression. While the male genitalic differences between the two species are as distinct as between any pair of lycosid species within the same species group, the pairing experiments demonstrate these differences do not prevent interspecific copulation.

Congeneric lycosids have been hybridized in laboratory experiments to study developmental patterns (FRANCESCOLI & COSTA 1992) and the inheritance of courtship behavior (STRATTON & UETZ 1986). But we know of no reports of natural hybridization in the Lycosidae.

The presence of both species as well as "intermediates" (Fig. 12) in the narrow overlap region makes it unlikely that the variation observed is some sort of steep geographic cline. Rather, it is likely that *L. ericeticola* allopatrically speciated during an early Pleistocene interglacial period when the sea level was significantly higher and small habitat (or real) islands were created along the eastern side of a partly submerged Florida peninsula (WEBB 1990, MAYR 1963). Climatic changes or human activities (such as land clearing in the 19th century) may have disturbed natural barriers allowing a relatively recent meeting of the two species. This would explain the apparent absence of effective premating isolating mechanisms between them. Such interspecific coupling would be a necessary, though not sufficient, condition for successful hybridization.

Thus we have a region of secondary intergradation, the result of recent secondary contact between two populations that would be recognized as distinct and separate species by the standard morphological criteria used in spider taxonomic work.

ACKNOWLEDGMENTS

We would like to thank Mr. Joe Judge, an undergraduate research assistant, for his meticulous work in taking the scanning electron microscopic photographs.

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Ergänzungen zur Kenntnis der litauischen Spinnenfauna I.

Vygandas RELYS
Lehrstuhl für Zoologie, Universität Vilnius, Ciurlionio 21/27, LT-2009 Vilnius, Litauen
Forschungsinstitut Gastein-Tauernregion, Haus Austria, A-5640 Badgastein, Österreich

Supplements to the knowledge of the spider fauna of Lithuania I. - The paper summarizes the informations from five publications including the data on spider fauna of Lithuania, where 12 species are new to Lithuania. The data on another new 32 species of spiders of Lithuania found in 1993 are presented. A total of 277 spider species is known from Lithuania.

Key-words: Araneae - checklist - faunistics - bibliography - Lithuania.

EINLEITUNG

In Rahmen der in Litauen laufenden arachnologischen Forschungen sind im Jahre 1993 einige Sammlungsexkursionen und kurzzeitige Barberfallenfänge durchgeführt worden. Dank des weißrußländischen Kollegens E. Zhukovetz ist es möglich geworden, Informationen über bisher in Litauen nicht berücksichtigte, die litauische Spinnenfauna betreffenden Arbeiten (DAHL 1908, 1926; DAHL & DAHL 1927; PERELESINA 1930; MIKHAILOV 1992) zu beziehen und nach entsprechender Überprüfung als Ergänzung zur Liste der Spinnen Litauens (RELYS 1994) anzuschließen.

ZUSÄTZLICHE LITERATURANGABEN

Zu den ältesten aus dem Territorium des heutigen Litauens erwähnten Angaben über die Spinnenfauna sollten die von F. DAHL im Sommer 1905 gesammelten und in späteren Publikationen (1908, 1926 und 1927) kommentierten Aufsammlungen gerechnet werden. DAHL (1908) erwähnt 24 Lycosiden-Arten, deren Fundorten (Bezirke Silute und Gargzdai, Stadt Klaipeda (Memel)) sich auch jetzt in Litauen gut feststellen lassen. Die die Springspinnen (Salticidae) Deutschlands behandelnde Arbeit (DAHL 1926) enthält Angaben über 6 aus denselben Fängen stammenden

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Arten. Die nächste Veröffentlichung über die Wolfspinnenfauna (Lycosidae) Deutschlands (Dahl & Dahl 1927) stellt nur einen Teil der im Jahre 1908 erwähnten Arten, sowie *Zora spinimana* (Sundevall) vor. Die von anderen Autoren für die Reihe "Die Tierwelt Deutschlands und der angrenzenden Meeresteile" über die diversen Spinnenfamilien verfaßten Bände enthalten keine genauere Hinweise auf diese von F. Dahl gesammelten Materialien. Insgesamt hat F. Dahl 32 Spinnenarten der Gattungen *Alopecosa* (4 Arten), *Arctosa* (2), *Hygrolycosa* (1), *Pardosa* (12), *Pirata* (2), *Trochosa* (2), *Xerolycosa* (2), *Dolomedes* (1), *Zora* (1), *Heliophanus* (1), *Pelenes* (1), *Sitticus* (2) und *Yllenus* (1) aus dem heutigen Territorium Litauens beschrieben, von denen die folgenden neun Arten nicht bei Relys (1994) aufscheinen:

Fam. Lycosidae

Alopecosa aculeata (Clerck, 1767) (Fundort: Silute)
Arctosa alpigena lamperti (Dahl, 1908) (Fundort: Augustumalmoor, Bez. Silute)
Pardosa nigriceps (Thorell, 1856) (Fundort: Silute)
Xerolycosa miniata (C.L. Koch, 1834) (Fundorte: Silute, Smiltyne/Klaipeda)

Fam. Salticidae

Heliophanus dampfi Schenkel, 1923 (Fundort: Augustumalmoor, Bez. Silute)
Sitticus distinguendus (Simon, 1868) (Fundort: Klaipeda)
Pelenes tripunctatus (Walckenaer, 1802) (Fundort: Smiltyne/Klaipeda)
Sitticus caricis (Westring, 1861) (Fundort: Augustumalmoor, Bez. Silute)
Yllenus arenarius Menge, 1868 (Fundort: Klaipeda)

In der Veröffentlichung von Perelesina (1930) sind Angaben über 31 in Litauen von N. Birschert im Jahre 1907 in der Umgebung der Siedlung Ukra, Bezirk Siauliai, von Winogradow-Nikitin in 1904–1906, in der Umgebung der Stadt Jurbarkas, sowie von Rydzewskij in 1910–1914 in der Umgebung von Vilnius gesammelten und von der Autorin determinierten den Familien Theridiidae (6 Arten), Linyphiidae (3), Tetragnathidae (4), Araneidae (5), Lycosidae (6), Pisauridae (1), Thomisidae (3), Salticidae (3) gehörenden Spinnenarten, notiert. Davon ist

Aelurillus v-insignitus (Clerck, 1757) (Fundort: Umgebungen von Vilnius

der Liste der litauischen Spinnen (Relys 1994) hinzuzufügen.

Mikhailov (1992) bringt neben der in der Liste litauischer Spinnen (Relys 1994) erwähnten Funde von verschiedenen *Clubiona*-Arten auch Angaben über die in dem Niedermoor-Seereservat "Zuvintas" Bez. Alytus gefundenen *C. juvenis* Simon, *C. lutescens* Westring und *C. norvegica* Strand, sowie auf der Vogelwarte Vente Bez. Silute nachgewiesenen *C. juvenis* Simon und *C. reclusa* O.P.- Cambridge. Davon sind zwei Arten

Clubiona juvenis Simon, 1878
Clubiona norvegica Strand, 1900

in die Liste der Spinnen Litauens (Relys 1994) einzufügen.

ERGÄNZENDE NEUFUNDE IM JAHRE 1993

Verwendete Abkürzungen:
Bez.- Bezirk (Kreis), Sdl.- Siedlung (Dorf), BF- Barberfallen.

THERIDIIDAE

Enoplognatha thoracica (Hahn, 1833)

1 ♂ 16.04–02.05.1993, BF. Junge trockene Heidekrautwiese (*Calluna vulgaris* Dominant). Sdl. Jaunadaris, Bez. Svencionys, Ostlitauen.

Pholcomma gibbum (Westring, 1851)

1 ♂, 1 ♀ 20.04–12.05.1993, BF. Grünmoos im reifen Kieferwald. Zalieji ezerai, Vilnius, Südostlitauen.

LINYPHIIDAE (ERIGONINAE)

Ceratinella brevipes (Westring, 1851)

3 ♂ 10.04–04.05.1993, BF. Nasser Schwarzerlenwald, Naturschutzgebiet "Artoji". Bez. Taurage, Westlitauen.

Diplocephalus permixtus (O.P.-Cambridge, 1871)

1 ♂ 10.04–04.05.1993, BF. Nasser Schwarzerlenwald, Naturschutzgebiet "Artoji". Bez. Taurage, Westlitauen.

Erigonella hiemalis (Blackwall, 1841)

1 ♂, 1 ♀ 16.04–02.05.1993, BF. Übergangsstelle von trockener Heidekrautwiese zum Birkenniedermoor. Sdl. Jaunadaris, Bez. Svencionys, Ostlitauen.

Gonatim rubellum (Blackwall, 1841)

1 ♀ 10.04–25.04.1993, BF. Nasser Schwarzerlenwald, Naturschutzgebiet "Artoji". Bez. Taurage, Westlitauen.

Lophomma punctatum (Blackwall, 1841)

4 ♂ 10.04–04.05.1993, BF. Nasser Schwarzerlenwald, Naturschutzgebiet "Artoji". Bez. Taurage, Westlitauen .

Metopobactrus prominulus (O.P.-Cambridge, 1872)

1 ♂ 14.05–06.06.1993, BF. Ruderalwiese in einer mit dem Klärschlamm rekultivierten Sandgrube. Sdl. Verksionys, Bez. Vilnius.

Micrargus herbigradus (Blackwall, 1854)

1 ♂ 10.04–04.05.1993, BF. Nasser Schwarzerlenwald, Naturschutzgebiet "Artoji". Bez. Taurage, Westlitauen.

Oedothorax apicatus (Blackwall, 1850)

15 ♂, 27 ♀ 14.05–06.06.1993; 1 ♂ 12.07–17.08.1994, BF. Ruderalwiese in einer mit dem Klärschlamm rekultivierten Sandgrube. Sdl. Verksionys, Bez. Vilnius.

Silometopus reussi (Thorell, 1871)

1 ♂, 2 ♀ 14.05–06.06.1993, BF. Ruderalwiese in einer mit dem Klärschlamm rekultivierten Sandgrube. Sdl. Verksionys, Bez. Vilnius.

Tiso vagans (Blackwall, 1834)

1 ♀ 06.06–28.06.1993, BF. Ruderalwiese in einer mit dem Klärschlamm rekultivierten Sandgrube; 1 ♀ 12.04–30.04.1993, BF. Grünmoos im Kieferwald. Beide in Sdl. Verksionys, Bez. Vilnius.

Walckenaeria antica (Wider, 1834)

4 ♂ 16.04–02.05.1993, BF. Übergangsstelle von trockener Heidekrautwiese zum Birkenniedermoor. Sdl. Jaunadaris, Bez. Svencionys, Ostlitauen.

2 ♀ 16.04–02.05.1993, BF. Junge trockene Heidekrautwiese (*Calluna vulgaris* Dominant) Sdl. Jaunadaris, Bez. Svencionys, Ostlitauen.

Walckenaeria alticeps (Denis, 1952)

2 ♂ 10.04–04.05.1993, BF. Nasser Schwarzerlenwald, Naturschutzgebiet "Artoji". Bez. Taurage, Westlitauen.

Walckenaeria dysderoides (Wider, 1834)

4 ♂ 10.04–04.05.1993, BF. Nasser Schwarzerlenwald, Naturschutzgebiet "Artoji". Bez. Taurage, Westlitauen.

Walckenaeria kochi (O.P.-Cambridge, 1872)

2 ♂ 10.04–04.05.1993, BF. Nasser Schwarzerlenwald, Naturschutzgebiet "Artoji". Bez. Taurage, Westlitauen.

Walckenaeria mitrata (Menge, 1868)

1 ♂ 16.04–02.05.1993, BF. Übergangsstelle von trockener Heidekrautwiese zum Birkenniedermoor. Sdl. Jaunadaris, Bez. Svencionys, Ostlitauen.

LINYPHIIDAE (LINYPHIINAE)

Bathyphantes parvulus (Westring, 1851)

1 ♂ 11.06–01.07.1994, BF. Nährstoffreiche Uferbrache des Flusses Levuo. Sdl. Pakuodziukai, Bez. Panevezys, Nordlitauen.

Centromerus incilium (L. Koch, 1881)

2 ♂, 4 ♀ 16.04–02.05.1993, BF. Übergangsstelle von trockener Heidekrautwiese zum Birkenniedermoor. Sdl. Jaunadaris, Bez. Svencionys, Ostlitauen.

Drepanotylus uncatus (O.P.-Cambridge, 1873)

1 ♀ 10.04–04.05.1993, BF. Nasser Schwarzerlenwald, Naturschutzgebiet "Artoji". Bez. Taurage, Westlitauen.

Lepthyphanthes angulipalpis (Westring, 1851)

1 ♂ 12.04–30.04.1994, BF. Grünmoos im jungen Kieferwald. Sdl. Verksionys, Bez. Vilnius.

Lepthyphanthes mengei Kulczynski, 1887

2 ♀ 12.04–30.04.1994, BF. Grünmoos im jungen Kieferwald. Sdl. Verksionys, Bez. Vilnius.

Macrargus rufus (Wider, 1834)

17 ♂, 5 ♀ 20.04–12.05.1994, BF. Grünmoos im reifen Kieferwald. Zalieji ezerai, Vilnius, Südostlitauen.

Stemonyphantes lineatus (Linnaeus, 1758)

7 ♂ 12.04–30.04.1994, BF. Offener dem Kieferwald angrenzender Sandhang einer Sandgrube. Sdl. Verksionys, Bez. Vilnius.

Tallusia experta (O.P.-Cambridge, 1871)

1 ♀ 10.04–04.05.1993, BF. Nasser Schwarzerlenwald, Naturschutzgebiet "Artoji". Bez. Taurage, Westlitauen.

HAHNIIDAE

Hahnia pusilla C.L. Koch, 1841

1 ♂ 16.04–02.05.1993, BF. Übergangsstelle von trockener Heidekrautwiese zum Birkenniedermoor. Sdl. Jaunadaris, Bez. Svencionys, Ostlitauen.

GNAPHOSIDAE

Zelotes clivicola (L. Koch, 1870)

4 ♂, 2 ♀ 16.04–02.05.1993, BF. Übergangsstelle von trockener Heidekrautwiese zum Birkenniedermoor. Sdl. Jaunadaris, Bez. Svencionys, Ostlitauen.

Zelotes exiguus (Müller & Schenkel, 1895)

1 ♂ 16.04–02.05.1993, BF. Junge trockene Heidekrautwiese (*Calluna vulgaris* Dominant). Sdl. Jaunadaris, Bez. Svencionys, Ostlitauen.

THOMISIDAE

Ozyptila scabricula (Westring, 1851)

1 ♂ 16.04–02 05.1993, BF. Junge trockene Heidekrautwiese (*Calluna vulgaris* Dominant). Sdl. Jaunadaris, Bez. Svencionys, Ostlitauen.

Xysticus kochi Thorell, 1872

18 ♂ 12.04–30.04.1994, BF. Grünmoos im jungen Kieferwald. Sdl. Verksionys, Bez. Vilnius.

SALTICIDAE

Euophrys aequipes (O.P.-Cambridge, 1871)

1 ♀ 16.04–02.05.1993, BF. Junge trockene Heidekrautwiese (*Calluna vulgaris* Dominant). Sdl. Jaunadaris, Bez. Svencionys, Ostlitauen.

Euophrys frontalis (Walckenaer, 1802)

4 ♂, 2 ♀ 16.04–02.05.1993, BF. Übergangsstelle von trockener Heidekrautwiese zum Birkenniedermoor. Sdl. Jaunadaris, Bez. Svencionys, Ostlitauen.

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REVUE SUISSE DE ZOOLOGIE, vol. hors série: 561-569; août 1996

Species composition and site distribution of spiders (Araneae) in a gneiss massif in the Dyje river valley

Vlastimil RUŽIČKA
Institute of Entomology, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic.

Species composition and site distribution of spiders (Araneae) in a gneiss massif in the Dyje river valley. - The species-rich community of spiders in boulder debris and crevice-type caves of the "Ledové Sluje" gneiss massif in the Dyje river valley in southern Moravia (Czech Republic) is described. The community comprises both relict and synanthropic species, and both thermophilous and psychrophilous species, according to highly segmented environment with a variety of microclimatic conditions. The species composition of the spider communities is characterized along the gradient from the boulder debris surface down a depth of approximately ten metres in crevices of the rock massif. The spider biomass and species diversity seems to decrease with increasing depth of the underground spaces. The dominant species are *Pholcus opilionoides* on the debris field surface, *Lepthyphantes improbulus* at depths about 0.5–5 m, and *Porrhomma egeria* at depths larger than 5 m. The occurrence of species with progressing morphological adaptations to life in subterranean environment in the boulder debris and cavities of the gneiss massif gives evidence that these underground spaces, also in non-karst areas, play an important part in the underground evolution of invertebrates.

Key-words: Rocks – stony debris – pseudokarst – caves – spiders – diversity – troglomorphisms.

INTRODUCTION

A highly diverse mosaic of microclimatic conditions occurs in slope boulder accumulations. Two important gradients establish, viz. between the upper and lower margins of the debris field and between the surface and inner spaces of the debris. Ecosystems of boulder debris can host isolated populations of invertebrates. Species exhibiting morphological adaptations to life in the subterranean environment have been found in depth of stony debris (RUŽIČKA & ZACHARDA 1994; RUŽIČKA *et al.* 1995).

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Proceedings of the XIIIth International Congress of Arachnology, Geneva, 3-8-IX.1995.

STUDY SITE AND METHODS

The Dyje Valley National Park lies on the boundary of the Česká Vysočina highland and the Carpathians, that is, the boundary of the Mesophyticum and the Pannonian Thermophyticum (HEJNY & SLAVIK 1988). The elevated western part is characterized by ample rains, whereas in the lower-altitude eastern part, where the average temperature is higher, rains are less frequent. The deeply incised valley of the Dyje river enables fauna and flora of the two systems to combine. Meander necks and sunny sites host thermophilous plants whose isolated islets penetrate deeply into the Mesophyticum; and on the other hand, inversion in the valley allows submountain species to descend to low altitudes. On bare rocks facing the north and on boulder accumulations, i.e. primarily forestless nonxerothermal sites, vegetation occurs which is closely related to some mountain or even subalpine vegetation types (CHYTRY 1992).

Some three km to the SE of the town Vranov nad Dyjí the river Dyje forms a meander bypassing a spur called "Ledové Sluje", which means "Ice Caves". The whole massif consists of heavily creviced orthogneiss. In its upper part the meander spur is rimmed by steep rock walls under which there stretches a ditch-like depression

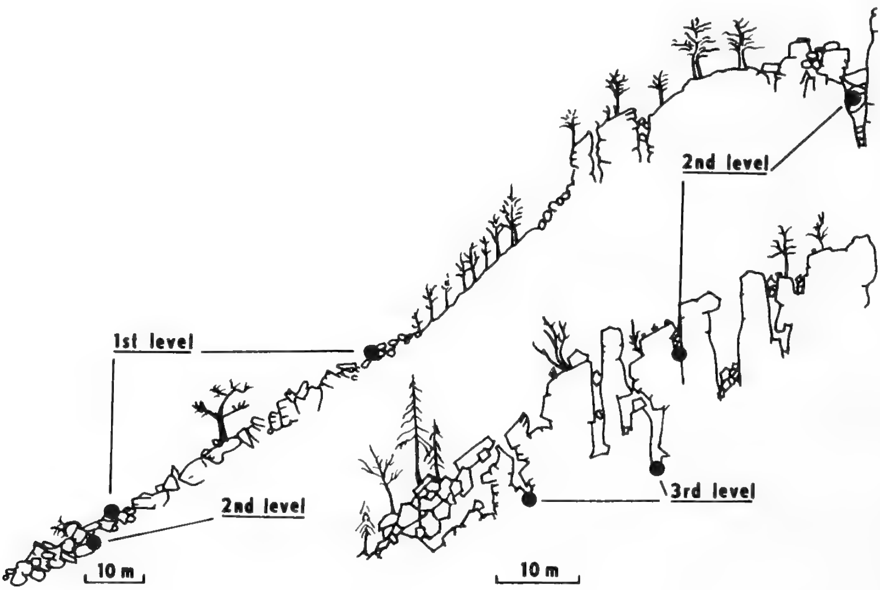

FIG. 1.
Schematic of the Ledové Sluje rocky spur profile (ZVELEBIL *et al.* 1996; KOPECKY 1996). Three space levels with characteristic dominant spider species are marked: 1st level – *Pholcus opilionoides*, 2nd level – *Lepthyphantes improbulus*, 3rd level – *Porrhomma egeria*.

covered by broken rock blocks. Down the slope, gravitational motion of blocks of the creviced rock massif has given rise to a system of crevice-type caves, lying as deep as tens of metres. In some of them, ice forms and persists till summer (JARZ 1882; ŠPALEK 1935). Below this region of pseudo-ice caves, a bare block field about 100 m long and 100 m broad lies on the northwestern slope. The blocks, which constitute a stony debris formation, are on average 250 cm in size. Isolated herb tussocks and dwarf trees grow in the debris field (Fig. 1). Appreciable cold air movement was observed under the blocks at the lower margin of the debris. The temperature, measured with a minimo-maximal thermometer, ranged from −16 to +8°C at cold air movement sites over the period from 25 November 1992 to 25 October 1993.

Spiders were collected in 1992–1994 by hand picking and by using modified pitfall traps (RUŽIČKA 1982, 1988). The traps were laid on the surface of the debris (3 traps), between boulders inside the debris (9 traps), in boulder accumulations in the cave entrances (5 traps), as well as in caves (5 traps), where they were left for approximately one year. A total of 268 spider individuals belonging to 76 species were collected (Table 1).

TABLE I

Survey of material collected at the Ledové Sluje site within the 1992–1994 period. Explanation see in Methods.

species			♂/♀/juv.
Pholcidae			
T	III	*Pholcus opilionoides* (Schrank, 1781)	10/10/9
Segestriidae			
P	II	*Segestria senoculata* (Linné, 1758)	1/2
Dysderidae			
T	I	*Dysdera ninnii* Canestrini, 1868	–/1/1
N	II	*Harpactea hombergi* (Scopoli, 1763)	–/1/3
P	II	— *lepida* (C.L. Koch, 1839)	–/1
T	III	— *rubicunda* (C.L. Koch, 1839)	–/2
Mimetidae			
N	II	*Ero furcata* (Villers, 1789)	–/1
Nesticidae			
?	III	*Nesticus cellulanus* (Clerck, 1757)	–/3/3
Theridiidae			
M	II	*Achaearanea lunata* (Clerck, 1757)	2/–
T	I	*Dipoena melanogaster* (C.L. Koch, 1845)	1/1
N	III	*Enoplognatha ovata* (Clerck, 1757)	2/–
N	II	*Episinus truncatus* Latreille, 1809	2/–
N	I	*Pholcomma gibbum* (Westring, 1851)	1/–
?	I	*Theonoe minutissima* (O. P.-Cambridge, 1879)	–/2
P	I	*Theridion bellicosum* (Simon, 1873)	–/1
N	III	— *bimaculatum* (Linné, 1767)	1/–
N	III	— *sisyphium* (Clerck, 1757)	1/1
N	III	— *varians Hahn*, 1833	1/–

Linyphiidae

P	I	*Agyneta conigera* (O. P.-Cambridge, 1863)	–/4
N	III	*Centromerus sylvaticus* (Blackwall, 1841)	–/3
P	II	*Lepthyphantes alacris* (Blackwall, 1853)	1/4
P	II	— *cristatus* (Menge, 1866)	2/–
P	I	— *improbulus* Simon, 1929	21/21
M	III	— *leprosus* (Ohlert, 1865)	7/8
P	II	— *nitidus* Thorell, 1875	–/1
P	I	— *nodifer* Simon, 1884	–/5
P	I	— *obscurus* (Blackwall, 1841)	1/–
N	II	— *pallidus* (O. P.-Cambridge, 1871)	–/2
N	III	*Meioneta rurestris* (C.L. Koch, 1836)	1/1
N	II	*Microneta viaria* (Blackwall, 1841)	–/2
M	II	*Neriene radiata* (Walckenaer, 1841)	2/6
P	I	*Porrhomma egeria* Smon, 1884	4/5/1
N	III	— *microphthalmum* (O. P.-Cambridge, 1871)	–/1
P	II	— *pallidum* Jackson, 1913	–/1
P	II	*Saaristoa firma* (O. P.-Cambridge, 1901)	–/1/1
N	II	*Ceratinella brevis* (Wider, 1834)	1/–
M	I	— *major* Kulczynski, 1894	1/1
N	III	*Diplocephalus cristatus* (Blackwall, 1833)	–/1
N	II	— *latifrons* (O. P.-Cambridge, 1863)	1/1
N	II	— *picinus* (Blackwall, 1841)	1/1
P	I	*Glyphesis servulus* (Simon, 1881)	1/–
M	I	*Kratochviliella bicapitata* Miller, 1939	5/3
P	II	*Maso sundevalli* (Westring, 1851)	–/1
P	III	*Micrargus herbigradus* (Blackwall, 1854)	5/1
?	I	*Pelecopsis nemoralis* (Blackwall, 1841)	1/1
N	II	*Trematocephalus cristatus* (Wider, 1834)	1/–

Tetragnathidae

P	III	*Meta menardi* (Latreille, 1804)	1/–/4
P	III	*Metellina merianae* (Scopoli, 1763)	–/–/1
N	III	*Pachygnatha degeeri* Sundevall, 1830	–/1

Araneidae

N	III	*Araniella cucurbitina* (Clerck, 1757)	–/3
N	III	*Araneus diadematus* Clerck, 1757	1/–
N	III	*Mangora acalypha* (Walckenaer, 1802)	1/–
T	I	*Zilla diodia* (Walckenaer, 1802)	3/–

Lycosidae

N	II	*Pardosa lugubris* (Walckenaer, 1802)	2/1
N	II	*Xerolycosa nemoralis* (Westring, 1861)	2/2

Agelenidae

N	III	*Cicurina cicur* (Fabricius, 1793)	3/1
P	II	*Histopona torpida* (C.L. Koch, 1834)	1/–
?	III	*Tegenaria ferruginea* Panzer, 1804	2/–
N	II	— *silvestris* L. Koch, 1872	2/2/1
N	II	*Textrix denticulata* (Olivier, 1789)	–/2

Dictynidae

T	I	*Bromella falcigera* (Balogh, 1935)	1/1

Amaurobiidae			
P	II	*Amaurobius fenestralis* (Stroem, 1768)	1/3
T	I	— *jugorum* (L. Koch, 1868)	1/–
P	II	*Callobius claustrarius* (Hahn, 1831)	2/1/1
Liocranidae			
N	III	*Liocranum rupicola* (Walckenaer, 1830)	3/–
M	I	— *rutilans* (Thorell, 1875)	1/1
N	II	*Phrurolithus festivus* (C.L. Koch, 1835)	–/1
Gnaphosidae			
N	II	*Drassodes lapidosus* (Walckenaer, 1802)	2/–
N	I	*Echemus angustifrons* (Westring, 1861)	1/3
Zoridae			
N	II	*Zora spinimana* (Sundevall, 1833)	–/1/1
Salticidae			
M	II	*Evarcha arcuata* (Clerck, 1757)	–/1
?	I	*Heliophanus aeneus* (Hahn, 1831)	–/4
T	II	— *cupreus* (Walckenaer, 1802)	1/–
?	I	— *melinus* L. Koch, 1867	1/–
M	II	*Neon reticulatus* (Blackwall, 1853)	2/–
N	III	*Salticus scenicus* (Clerck, 1757)	–/1

The material was identified and evaluated with respect to the occurrence of the species in phytogeographical regions and in habitats of various degree of originality (BUCHAR 1992): T – occurring prevailingly in western part of Thermophyticum, M – occurring prevailingly in Mesophyticum, O – occurring prevailingly in Oreophyticum, N – non-specific. I – occurring in natural habitats corresponding to climatic or edaphic climax, II – species capable of occupying some shadow and wet secondary, semi-natural habitats (cultural forests, shrubs, cultivated wetlands), III – species capable of forming viable populations in artificially deforested, man-made habitats (fields, meadows, spoil banks, and urban biotopes). For the specimens in traps, the spider activity (after RUŽIČKA 1987*a*), spider dry weight (after BREYMEYER 1969) and Shannon's index of diversity were caltulated.

RESULTS AND DISCUSSION

The frequency of specimens of species occurring prevailingly in natural habitats in the collection from pitfall traps is 0.43, which is considerably higher than the minimal value of 0.20 that is characteristic for protected regions in the Czech Republic (RUŽIČKA 1987*b*), despite the fact that the site hosts the following hemisynanthropic species (sensu SACHER 1983): *Harpactea rubicunda*, *Segestria senoculata*, *Lepthyphantes leprosus*, *Nesticus cellulanus*, *Liocranum rupicola*, *Amaurobius fenestralis*, and *Salticus scenicus*. Those are species which are classed as "occupying man-made biotopes" in BUCHAR's categorization (BUCHAR 1992). Actually, however,

typical opportunistic species of this category inhabit unstable environment, such as sites of field cultures; they are typical r-strategists with a high reproductive potential and a high spreading capacity. Hemisynanthropic species, on the other hand, inhabit relatively stable environment of human dwellings, which is not dissimilar to the natural stable environment of stony and rocky biotopes. The group of hemisynanthropic species could be classified as separate group. Simultaneous occurrence of relict and synanthropic species is a characteristic feature of stony debris (RUŽIČKA 1989).

The whole collection contains 21 species occurring prevailingly in original habitats. Five of those, viz. *Dysdera ninnii*, *Dipoena melanogaster*, *Zilla diodia*, *Bromella falcigera*, and *Amaurobius jugorum* were found principally in Thermophyticum, whereas other seven, viz. *Theridion bellicosum*, *Agyneta conigera*, *Lepthyphantes improbulus*, *L. nodifer*, *L. obscurus*, *Porrhomma egeria*, and *Glyphesis servulus* seem to prefer the Oreophyticum. Simultaneous occurrence of species of these two categories in stony debris has already been observed by BUCHAR *et al.* (1979) and by RUŽIČKA (1989, 1994). Hence, stony biotopes with many underground cavities contribute significantly to the biodiversity of landscape (RUZICKA 1993). What are the causes for the observed species diversity?

The northwestern orientation, owing to which the site is partly sunny, facilitates the occurrence of thermophilous species, which occupy the surface boulder layer heated by solar rays (*Dysdera ninnii*, *Amaurobius jugorum*). Isolated trees and vegetation tussocks do not shade the stony debris and enable thermophilous web-forming species (*Dipoena melanogaster*, *Zilla diodia*) to live there. Air movement through the extensive system of underground cavities is responsible for an all-year cold microclimate at the lower margin of the debris field. Owing to this, the psychrophilous species *Agyneta conigera*, *Lepthyphantes nodifer*, *L. obscurus*, and *Glyphesis servulus* are found there in moss and detrite.

The decaying gneiss massif forms a wide variety of underground spaces. The spider biomass as well as the species diversity seems to decrease from the surface downwards (Table 2). With respect to the species composition similarity, three space levels were detect (Table 3, Fig. 1). *Pholcus opilionoides* is the dominant species on the debris surface, *Lepthyphantes leprosus* is here also numerous. *Lepthyphantes improbulus* is the most abundant species in the material. It was observed in all the spaces examined, with a maximum occurrence at 2–3 m depths, under blocks and in the entrance holes of the caves, at sites with fine soil. *Porrhomma egeria* only occured in deep lying caves of the massif, at depths larger than 5 m where soil is rather compact and is wet constantly.

Morphological adaptations to life in caves – troglomorphisms (sensu ZACHARDA 1979) – are known for two of the species observed. MORITZ (1972) found that in comparison with specimens trapped in Pyrenean forests, the central European populations of *Lepthyphantes improbulus* have longer legs and their eye lenses are less bulged. *Porrhomma egeria* is the only spider species occupying regularly deep cavernous spaces in central Europe. SANOCKA (1982) described a gradual eye reduction for this species in dependence on the site distance from the cave entrance.

TABLE 2

Survey of characteristics of spider material from pitfall traps. No – number of a trap, D – depth (m), A – activity ($ind.m^{-1}.year^{-1}$), W – dry weight ($mg.m^{-1}.year^{-1}$), H' – Shannon's index of diversity. Correlation coefficients: A: -0.31, $p = 0.155$; W: -0.51, $p < 0.05$; H': -0.48, $p < 0.05$.

No	1	2	3	4	5	6	7	8	9	10	11
D	0	0	0	0.4	0.5	0.7	0.7	1.5	1.5	2	2
A	44	62	56	21	12	9	9	3	24	44	27
W	337	167	187	72	8	7	159	2	111	50	140
H'	2.2	2.7	3.1	2.5	1.5	0.9	0.9	0	2.3	2.3	2.8

No	12	13	14	15	16	17	18	19	20	21	22
D	2	2	2	2.5	3	3	6	7	7	10	10
A	6	81	29	33	20	16	34	12	24	4	16
W	136	37	93	57	86	48	50	32	27	2	8
H'	1.0	1.8	1.8	1.6	1.4	1.5	2.5	1.6	1.8	0	0

TABLE 3

Survey of species tied to stony and underground biotopes as caught in pitfall traps (numbers of specimens in three depth levels).

species	surface	0.5–5 m	5–10 m
Pholcus opilionoides	20	—	—
Echemus angustifrons	4	—	—
Liocranum rupicola	3	—	—
Liocranum rutilans	2	—	—
Drassodes lapidosus	2	—	—
Heliophanus aenaeus	1	—	—
Histopona torpida	1	—	—
Tegenaria ferruginea	1	—	—
Porrhomma pallidum	1	—	—
Theonoe minutissima	1	—	—
Lepthyphantes leprosus	10	5	—
Segestria senoculata	1	1	—
Tegenaria silvestris	2	3	—
Theridion bellicosum	—	1	—
Meta menardi	—	3	—
Cicurina cicur	—	4	—
Kratochviliella bicapitata	2	2	3
Lepthyphantes improbulus	3	32	2
Nesticus cellulanus	—	5	1
Lepthyphantes alacris	—	1	2
Lepthyphantes nitidus	—	—	1
Porrhomma egeria	—	—	10

Hence, two spider species exhibiting a process of adaptation to life underground have been observed in stone block debris and crevices in the massif at the Ledové Sluje site. This documents the importance of shallow subterranean spaces for the underground evolution of invertebrates, and disproves the hypothesis that only deep karst caves are of importance to this evolution (VANDEL 1965).

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Composition of the araneofauna of the Cape Verde Islands

Günter SCHMIDT
Von-Kleist-Weg 4, D-21407 Deutsch Evern, Germany.

Composition of the araneofauna of the Cape Verde Islands. - From the Cape Verde Islands 25 families of spiders with 116 species are recorded. About 50% of them have to be considered as endemics. Some of these species are related to others from the Palaearctic and the Afrotropical region. 52 species can be used for a biogeographical analysis. 25 out of the 116 Cape Verdean species are also found on the Makaronesian Islands, 22 of the 23 transgressing species occur in the Mediterranean area. 13 species have a cosmopolitan or circumtropical distribution and 11 species are found in the Afrotropical region. Only four species live exclusively on the Makaronesian Islands. Six of 11 Araneidae show a distribution extending over more than one continent. 17 species live as synanthropics, 12 of them are cosmopolitans. The most surprising result is the low number of Afrotropical species in comparison to the high amount of species also present on other Atlantic islands and in the Mediterranean region, although the Cape Verde Islands belong to the Afrotropical region.

Key-words: Cape Verde Islands - Makaronesian Islands - Araneida - biogeography - faunistics.

INTRODUCTION

The Cape Verde Islands belong to the tropics and consist of 9 inhabited and 6 uninhabited islands, situated between 15 and 17 degrees north, about 500 km west off the coast of Senegal. The distance to the Canary islands is about 1500 km, to Madeira about 2200 km and to the Açores about 2500 km. They are situated between the 20°C and the 25°C isotherm, which corresponds with the Canary Islands and the North African Mediterranean area. Biogeographically they represent the border between the Palearctic and the Afrotropical region. On account of the situation and the climate one can expect spiders living in the tropics, on the Makaronesian Islands (Canary Islands, Madeira, Açores), in the Mediterranean area of North Africa and in the area south of the Sahara.

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BERLAND (1936) was the first arachnologist who studied the relationships of the spider fauna of the Cape Verde Islands. 25 species out of the 48 known at that time were considered as endemic ones, 12 transgressing from the Mediterranean area, eight cosmopolitans and only three were known from the Afrotropical region. 46 years later ASSMUTH & GROH (1982) listed 67 species and classified 26 of them. 13 were mediterranean, seven cosmopolitan, four of Afrotropical and two of Makaronesian origin.

As a result of my 5 expeditions (1988–1995) the number of species increased to 116. Therefore a new biogeographical survey seems of interest, because we can consider more than twice as many species as BERLAND could.

MATERIAL AND METHODS

Collecting was exclusively done by hand because time was not sufficient for other methods. Immature spiders were brought alive to Germany to rear them to maturity. The spiders were preserved in 70% alcohol. Genitals were prepared by embedding them in polyvinyllaktophenol if necessary. The material was deposited in the Senckenbergmuseum, Frankfurt/M., Germany.

RESULTS

25 families containing 116 species are present on the Cape Verde Islands (table 1). The Families with the highest number of species are Theridiidae (18 species), Salticidae (16 species), Gnaphosidae (16 species) and Araneidae (11 species).

Out of 116 species 52 can be classified for biogeographical purposes. The remaining ones are either endemics or could not be named up to now. Some of the endemic species are related to species from the Palearctic region and from Senegal.

As table 2 shows, 26 Cape Verdean species live also on the Makaronesian Islands. 25 of them are inhabitants of the Canary Islands. Five of them belong to the Theridiidae.

21 of the 22 transgressing species occur in the Mediterranean area. Only *Neoscona moreli* (Vinson, 1863) has an exclusively tropical distribution. 13 species have a cosmopolitan or circumtropical distribution. Among the latter one could find in the past *Tegenaria domestica* (Clerck, 1757), but recent studies on the genitalia have shown that the *Tegenaria* of the Cape Verde Islands is another species living in the field and away from buildings (SCHMIDT *et al.*, 1994).

Five of the 11 Afrotropical species belong to the Araneidae. The Makaronesian species – living exclusively on one or more islands of the three archipelagos mentioned above – represent the smallest group of the Cape Verdean spiders. Four species belong to this group, all exist on the Canarian Islands. *Tidarren chevalieri* (Berland, 1936) was described from the Cape Verde Islands. According to WUNDERLICH (1991) *Tidarren hagemanni* Schmidt, 1956 (syn. *Tidarren pseudogibberosum* Schmidt, 1973) from the Canary Islands is a synonym of *T. chevalieri*. This judgement was made

without taking in account the male of this species, described not until 1994. The comparison between the males of *T. chevalieri* and *T. hagemanni* shows that the radix of the palpus in *T. hagemanni* is wider than in *T. chevalieri*. Therefore there is some doubt concerning this synonymy. The low number of Makaronesian species on the Cape Verde Islands confirms the statement of many entomologists that these islands do not belong to Makaronesia.

The synanthropic species (17) are the third biggest group of the Cape Verdean spiders. 12 of them are cosmopolitans. Only two are endemics.

The orb-weaving spiders are the most conspicuous ones of the Cape Verde Islands. Six of the Araneidae show a distribution extending over more than one continent.

DISCUSSION

Our study could confirm the statements given by Berland (1936) and Assmuth & Groh (1982) that about 50% of the spiders of the Cape Verde Islands might be considered as endemics and that the Mediterranean species are the richest group of the remaining ones. The number of the cosmopolitans has changed only slightly.

The most surprising result of this study is the low number of Afrotropical species in comparison to the high amount of the species present also on the other Atlantic islands and in the Mediterranean region. Although the number of Afrotropical species could be increased from three respectively four to 11 the relation between the Mediterranean and the Afrotropical group could only be altered from 4:1 respectively 3:1 to approximately 2:1.

Table 1

Families and species of the Cape Verdean spiders

Agelenidae	*Tegenaria domesticoides* Schmidt & Piepho
Araneidae	*Afraranea rufipalpis* (Lucas)
	Afraranea triangula (Keyserling)
	Argiope sector (Forskal)
	Cyclosa insulana (Costa)
	Cyrtophora citricola (Forskal)
	Meta maculata (Blackwall)
	Neoscona moreli (Vinson)
	Neoscona subfusca (C.L. Koch)
	Nephila s. senegalensis (Walckenaer)
	Pararaneus spectator (Karsch)
	Tetragnatha torrensis Schmidt & Piepho
Clubionidae	*Cheiracanthium furculatum* Karsch
	Cheiracanthium halophilum Schmidt & Piepho
	Cheiracanthium mildei C.L. Koch
	Clubiona chevalieri Berland
	Clubiona sp.
	? *Tecution* sp.

Dysderidae	*Dysdera vermicularis* Berland
	Dysdera sp.
Filistatidae	*Filistata* sp.
Gnaphosidae	*Australoechemus celer* Schmidt & Piepho
	Australoechemus oecobiophilus Schmidt & Piepho
	Berlandina atlantica (Dalmas)
	Berlandina nigromaculata (Blackwall)
	Berlandina piephoi Schmidt
	Camillina sp.
	Drassodes assimilatus (Blackwall)
	Haplodrassus sp. n.
	Micaria sp.
	Scotophaeus bifidus Schmidt & Krause
	Scotophaeus insularis Berland
	Scotophaeus jacksoni Berland
	Scotophaeus typhlus Schmidt & Piepho
	Setaphis atlantica (Berland)
	Setaphis fibulata (Berland)
	Zelotes salensis Berland
Hersiliidae	*Hersiliola simoni* (Cambridge)
	Hersiliola versicolor (Blackwall)
Heteropodidae	*Heteropoda venatoria* (Linné)
Linyphiidae	*Koinothrix pequenops* Jocqué
	Meioneta sp.
Loxoscelidae	*Loxosceles rufescens* (Dufour)
Lycosidae	*Allocosa caboverdensis* Schmidt & Krause
	Arctosa variana C.L. Koch
	Lycorma ferox (Lucas)
	Lycosa sp.
	Pardosa aquatilis Schmidt & Krause
	Tricca sp.
Oecobiidae	*Oecobius annulipes* Lucas
	Uroctea paivai (Blackwall)
Oonopidae	*Orchestina pavesii* (Simon)
Oxyopidae	*Oxyopes caboverdensis* Schmidt & Krause
	Oxyopes crassus Schmidt & Krause
	Oxyopes heterophthalmus Latreille
	Peucetia viridis (Blackwall)
Philodromidae	*Ebo patellidens* Levy
	Philodromus bicornutus Schmidt & Krause
	Philodromus petrobius Schmidt & Krause
	Thanatus atlanticus Berland
	Thanatus frederici Denis
	Thanatus vulgaris (Simon)
Pholcidae	*Artema atlanta* Walckenaer
	Micropholcus fauroti (Simon)
	Smeringopus pallidus (Blackwall)
Pisauridae	*Perenethis simoni* (Lessert)
Salticidae	*Bianor albobimaculatus* (Lucas)
	Bianor marionis Schmidt & Krause
	Bianor pulchellus Wesolowska & van Harten
	Bianor simplex (Blackwall)
	Dendryphantes sedulus (Blackwall)
	Euophrys sp.
	Hasarius adansoni (Audouin)
	Hyllus dubius (Wesolowska)
	Luxuria lymphatica Wesolowska
	Menemerus bivittatus (Dufour)

	Pellenes sp.
	Phlegra bifurcata Schmidt & Piepho
	Plexippus lepidus (Blackwall)
	Stenaelurillus nigricauda Simon
	? sp. 1
	? sp. 2
Scytodidae	*Scytodes fusca* Walckenaer
	Scytodes major Simon
	Scytodes velutina Heineken & Lowe
Selenopidae	*Selenops radiatus* Latreille
Tetrablemmidae	gen. indet.
Theridiidae	*Anelosimus aulicus* (C.L. Koch)
	Argyrodes argyrodes (Walckenaer)
	Argyrodes scapulatus Schmidt & Piepho
	Coleosoma floridanum Banks
	Coleosoma africanum Schmidt & Krause
	Latrodectus cinctus Blackwall
	Latrodectus geometricus C.L. Koch
	Latrodectus geometricus "black"
	Latrodectus pallidus (O.P. Cambridge)
	Nesticodes rufipes (Lucas)
	Paidiscura dromedaria (Simon)
	Steatoda fallax (Blackwall)
	Steatoda quinquenotata (Blackwall)
	Steatoda sagax (Blackwall)
	Theridion musivivoides Schmidt & Krause
	Theridion luteitarsis Schmidt & Krause
	Theridion sp.
	Tidarren chevalieri (Berland)
Thomisidae	*Misumenops spinulosissimus* (Berland)
	Thomisus citrinellus Simon
	Thomisus hilarulus Simon
	Thomisus machadoi Comellini
	Xysticus blackwalli Roewer
Uloboridae	*Uloborus gnavus* (Blackwall)
	Uloborus luteolus (Blackwall)
	Uloborus plumipes Lucas
	Uloborus rufus Schmidt & Krause
	Zosis geniculatus (Olivier)
Zodariidae	*Zodarion* sp.

TABLE 2

Faunistic composition of the Cape Verdean spiders

(+ = Canary Islands, o = Madeira, x = Açores, 1) = cosmopolitan or circumtropical species, 2) = species of the Afrotropical region, 3) = Makaronesian species, 4) = synanthropic species)

Afraranea rufipalpis 2) (Tropical Africa, South Africa)
A. triangula 2) (Tropical Africa)
Anelosimus aulicus + o (Central Europe, Mediterranea, North Africa-Middle East)
Arctosa variana (Mediterranea)
Argiope sector 2) (Tropical Africa, Yemen)
Argyropes argyropes + o (Mediterranea, West Africa, Seychelles)
Artema atlanta 1) 4)
Bianor albobimaculatus (Mediterranea)
B. pulchellus 2) (Yemen)

Cheiracanthium furculatum 2) (West Africa)
C. mildei x 4) (Northern temperate zones of the world)
Coleosoma floridanum 1)
Cyclosa insulana + o (Mediterranea, Australia)
Cyrtophora citricola + o (Old World)
Drassodes assimilatus + 3)
Ebo patellidens + (North Africa - Israel)
Hasarius adansoni + 1) 4)
Hersiliola simoni (Mediterranea, Nigeria, Iraq)
Heteropoda venatoria 1) 4)
Latrodectus cinctus 2) (Tropical Africa, South Africa)
L. geometricus 1) 4)
L. geometricus "black" 2) (Tropical Africa, South Africa)
L. pallidus (Libya - Turkmenia)
Loxosceles rufescens + o 1) 4)
Lycorma ferox + (Mediterranea)
Luxuria lymphatica 4) (Cape Verde Islands)
Menemerus bivittatus + (?) 1) 4)
Micropholcus fauroti 1) 4)
Neoscona moreli (Tropical Africa, Antilles)
N. subfusca + o (Mediterranea - whole Africa)
Nephila senegalensis senegalensis 2) (West Africa)
Nesticodes rufipes + o x 1) 4)
Oecobius annulipes + o x 1) 4)
Orchestina pavesii + (Mediterranea)
Paidiscura dromedaria + (Mediterranea, Yemen)
Pararaneus spectator 2) (Niger, Sudan, Yemen, Somalia, Ethiopia, Mozambique, Zaire, Congo, Tansania, Kenia, Malawi, South Africa)
Perenethis simoni 2) (West-, Middle, East Africa, Comoro Islands)
Peucetia viridis (Mediterranea, West Africa)
Scytodes fusca 1) 4)
S. major (North Africa, Senegal, Equatorial Guinea)
S. velutina (Mediterranea, Africa, Arabia)
Selenops radiatus 4) (Mediterranea, Africa, India, Burma)
Smeringopus pallidus 1) 4)
Stenaelurillus nigricauda + 2) (Senegal)
Thanatus vulgaris + o (Northern temperate zones of the world)
Theridion musivivoides 4) (Cape Verde Islands)
Thomisus citrinellus (Mediterranea - South Africa, Seychelles)
T. hilarulus + (Mediterranea)
Tidarren chevalieri + 3) 4)
Uloborus plumipes + (Old World)
Uroctea paivai + 3)
Zosis geniculatua + o 1) 4)

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The fauna of orthognathous spiders (Araneae: Mesothelae, Mygalomorphae) in Thailand

Peter J. SCHWENDINGER
Institute of Zoology and Limnology, Technikerstr. 25, A-6020 Innsbruck, Austria.

The fauna of orthognathous spiders (Araneae: Mesothelae, Mygalomorphae) in Thailand. - The records of orthognathous spiders from Thailand are summarized; 34 species in 19 genera and 9 families are listed. Missing taxa and zoogeographical relations are discussed.

Key-words: Mesothelae - Mygalomorphae - Thailand - species list - zoogeography.

INTRODUCTION

As Thailand was never under colonial rule, it has been greatly neglected by western collectors in former times, who otherwise profusely supplied European museums with specimens. The catalogue of ROEWER (1942) mentions only three species of orthognathous spiders from this country: *Haplopelma albostriatum* Simon, *Chilobrachys paviei* Simon (both Theraphosidae), *Calommata obesa* Simon (Atypidae). No additional entries were given in the catalogue of BRIGNOLI (1983), but in their revision of the genus *Cyclocosmia*, GERTSCH & PLATNICK (1975) mentioned *C. ricketti* (Pocock) (Ctenizidae) to occur in China and Thailand. BRISTOWE (1975) reported *Liphistius* from northern Thailand but erroneously attributed it to *L. birmanicus* Thorell. PLATNICK & SEDGWICK (1984), however, correctly described it as a new species, *L. bristowei*, together with *L. trang* from southern Thailand.

Such was the poor state of knowledge of the orthognathous spiders in Thailand when I started research on these animals for my doctoral thesis at Chiang Mai University in 1985 (SCHWENDINGER 1988, 1990*a*). After completion, I had the opportunity to return to this country several times in the course of the "University Partnership Network, Austria - Southeast Asia". Results obtained by various colleagues and myself during the last 10 years have substantially extended our knowledge of this fauna. A brief summary is given in the following.

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Species list

Liphistiidae

Liphistius (18 spp.): *Liphistius bristowei* Platnick & Sedgwick, *L. trang* Platnick & Sedgwick (Platnick & Sedgwick 1984), *L. yamasakii* Ono, *L. jarujini* Ono, *L. bicoloripes* Ono, *L. schwendingeri* Ono, *L. niphanae* Ono (Ono 1988*a*, *b*), *L. owadai* Ono & Schwendinger, *L. ochraceus* Ono & Schwendinger, *L. ornatus* Ono & Schwendinger (Ono & Schwendinger 1990), *L. tham* Sedgwick & Schwendinger (Sedwick & Schwendinger 1990), *L. lannaianus* Schwendinger, *L. marginatus* Schwendinger, *L. thaleban* Schwendinger, *L. albipes* Schwendinger, *L. castaneus* Schwendinger, *L. fuscus* Schwendinger, *L. rufipes* Schwendinger (Schwendinger 1990*b*, 1995). *Liphistius rufipes* occurs also in peninsular Malaysia, all other species listed are known solely from Thailand. Eight new species from western and eastern Thailand will be described soon (Schwendinger, in preparation). Distribution see Fig. 1.

Atypidae

Calommata obesa, described from Bangkok (Simon 1886; type specimen examined), appears identical with *C. sundaica* (Doleschall, 1837), distributed in Java and Sumatra. Additional localities were found in northern and northeastern Thailand.

Atypus (3 spp.): *Atypus dorsualis* Thorell was described from the Karen State, eastern Burma and later found in northern Thailand (Schwendinger 1989). More populations have become known from the northeast; one male from there probably belongs to a new species. *Atypus suthepicus* Schwendinger and *A. lannaianus* Schwendinger are known from northern Thailand (Schwendinger 1989).

Hexathelidae

Macrothele spp: Two distinct species are present, one in the north, the other (probably *M. maculata* Thorell, described from eastern Burma) in almost all parts of Thailand.

Dipluridae

Phyxioschema suthepium Raven & Schwendinger was described from northern Thailand, further populations were later found in the western, central and southeastern regions (Raven & Schwendinger 1989, 1995).

Leptothele bencha Raven & Schwendinger occurs in southern Thailand (Raven & Schwendinger 1995).

Idiopidae

Idiops pylorus Schwendinger is known from northern and western Thailand (Schwendinger 1991); a further species was discovered in the northeast.

Prothemenops siamensis Schwendinger was described from the northeast (SCHWENDINGER 1991); several undescribed species of this genus were found in all parts of Thailand, except in the south. A population from the southeastern region was seen heavily infected by the pathogenic fungus *Nomuraea atypicola* (Yasuda) Samson (Deuteromycotina).

CTENIZIDAE

Cyclocosmia ricketti was reported from northeastern (GERTSCH & PLATNICK 1975) and northern Thailand (HUBER 1995); a second species occurs in the northeast.

Conothele spp: Several undescribed species occur in all parts of the country.

Latouchia sp. was collected at few localities in the south and east.

CYRTAUCHENIIDAE

Angka hexops Raven & Schwendinger is present in northern Thailand (RAVEN & SCHWENDINGER 1995).

NEMESIIDAE

Damarchus spp: Several undescribed species occur in all parts of the country.

Atmetochilus sp. was collected at two localities in the west and northeast.

Sinopesa maculata Raven & Schwendinger was recently described from northern Thailand, together with a congeneric species from southeastern China (RAVEN & SCHWENDINGER 1995).

THERAPHOSIDAE

Haplopelma (2 spp.): *Haplopelma minax* (Thorell), known from eastern Burma, is common in northern, western and southern Thailand (conspecific?). *Haplopelma albostriatum*, described from the "provinces de Vatena et de Zabin, Siam" (SIMON 1886; probably today's Watthana Nakhon, Sa Kaeo Province, and Kabin Buri, Prachin Buri Province, both in southeastern Thailand), is widespread in the central and eastern regions.

Cyriopagopus sp. (probably *C. paganus* Simon, reported from eastern Burma) was collected in northern and western Thailand.

Chilobrachys paviei was described from "Vatena" (= Watthana Nakhon) (SIMON 1886). The spiders I collected in northern Thailand apparently belong to *C. pococki* (Thorell), known from eastern Burma.

Phlogiellus spp: Several undescribed species were found to be common everywhere in Thailand.

At present 34 described species and 19 genera from 9 families (system according to RAVEN 1985) of orthognathous spiders are known from Thailand. The above list,

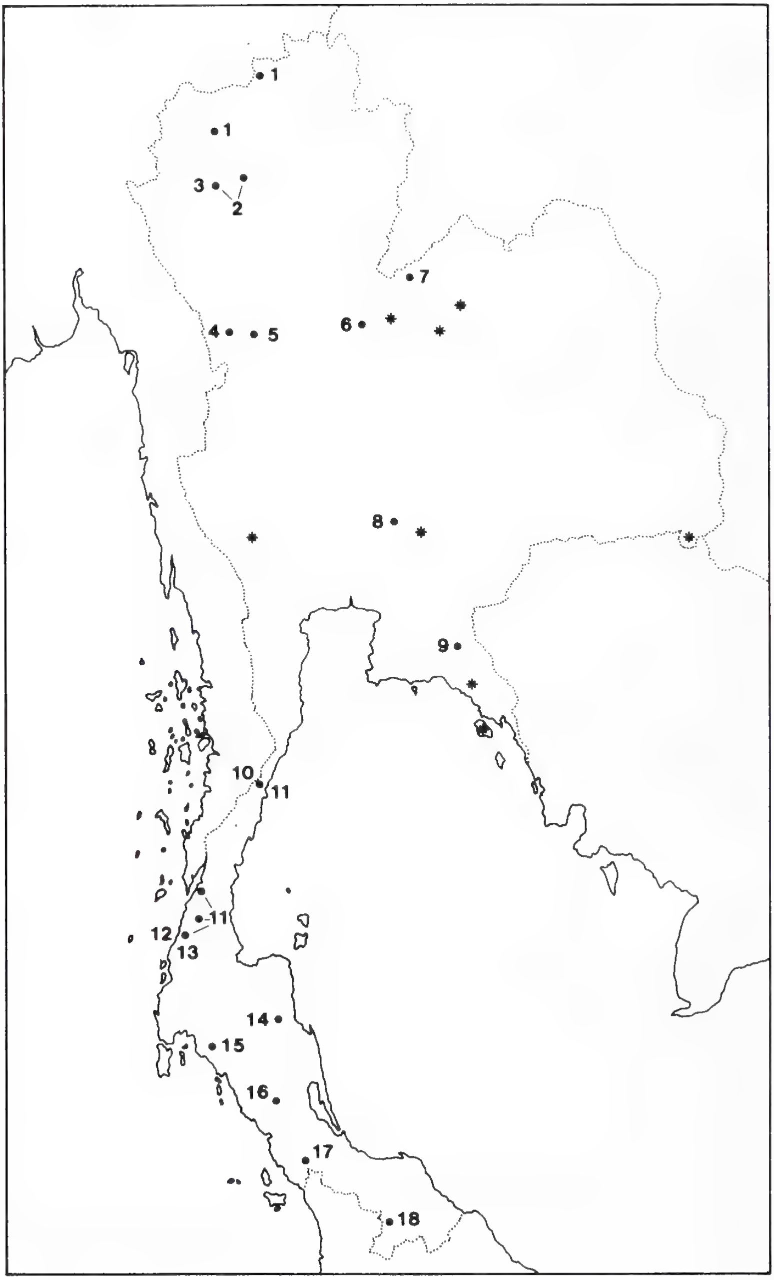

FIG. 1

Distribution of *Liphistius* in Thailand. 1 - *L. lannaianus*, 2 - *L. bristowei*, 3 - *L. yamasakii*, 4 - *L. jarujini*, 5 - *L. marginatus*, 6 - *L. owadai*, 7 - *L. ochraceus*, 8 - *L. tham*, 9 - *L. ornatus*, 10 - *L. albipes*, 11 - *L. bicoloripes*, 12 - *L. castaneus*, 13 - *L. schwendingeri*, 14 - *L. niphanae*, 15 - *L. fuscus*, 16 - *L. trang*, 17 - *L. thaleban*, 18 - *L. rufipes*. Asterisks show localities of new species (Schwendinger, in preparation).

however, is far from complete. In several genera, species cannot be determined; extensive taxonomic studies need to be done and many unnamed species await description. Moreover, some taxa are not yet known from Thailand, which can be expected to be present. The most obvious gap is the apparent lack of the Barychelidae, of which four species are known from Southeast Asia. *Rhianodes atratus* Thorell occurs on Penang Island and Maxwell Hill (Taiping, Perak), in the north of peninsular Malaysia (RAVEN 1994; Maxwell Hill erroneously listed in Singapore), as well as in Singapore (conspecific?). *Sipalolasma ophiriensis* Abraham, *S. aedificatrix* Abraham and *Idioctis litoralis* Abraham were described from Singapore and Johore, in the south of peninsular Malaysia (ABRAHAM 1924). These or related species may also live in the rain forests of southern Thailand.

Presumably more theraphosid genera are present than listed above, which reflects my general neglect towards this family. *Ornithoctonus*, *Selenocosmia*, *Coremiocnemis*, *Lampropelma* and *Lyrognathus* were all reported from areas adjacent to Thailand (POCOCK 1900; ABRAHAM 1924; SMITH 1988).

ZOOGEOGRAPHY

Thailand lies in the centre of mainland Southeast Asia, stretching about 1600 km in north-south direction. It encloses tropical regions with climatic conditions from seasonally dry to perhumid, as well as a wide range of habitats populated by orthognathous spiders, e.g. savannas, pinewoods, dry dipterocarp forests, rain forests, evergreen montane forests, cloud forests, mangroves and limestone caves. Furthermore, climatic and floristic changes during the Pleistocene have presumably led to a series of allopatric speciations in spiders with poor dispersal capabilities, as will be discussed for *Liphistius* (Schwendinger, in preparation). Such conditions are favourable for the development of a divers spider fauna, which is as yet largely unknown. The preliminary list of orthognathous spiders presented here gives a first impression of what is present.

Few genera of orthognathous spiders seem to be restricted to the Indochinese Subregion within the Oriental Region. These are *Atmetochilus* (Burma, Thailand), *Sinopesa* (southeastern China, Thailand) and *Prothemenops*. The latter is hitherto known only from Thailand (not in the south), but probably also occurs in neighbouring countries (Burma, Laos, Cambodia). Surprisingly the closest relatives of *Prothemenops* are members of the endemic Australian tribe Aganippini (Arbanitinae) and not of the Genysinae from India and Madagascar. A similar remarkable relationship with the Australian spider fauna was shown between *Angka* from northern Thailand and the Australian relict genus *Kiama* (RAVEN & SCHWENDINGER 1995).

Leptothele from southern Thailand (with a similar form recently discovered in northern Malaysia) appears to be Sundaic. Thailand, south of the Isthmus of Kraburi, is considered to be part of the Sundaic Subregion.

An Indochinese – Sundaic distribution is seen in *Haplopelma* [Burma, Thailand, Vietnam (von WIRTH 1991), peninsular Malaysia], *Cyriopagopus* (Burma,

Thailand, peninsular Malaysia) and *Liphistius* (Burma, Thailand, peninsular Malaysia, Sumatra). The known distribution of *Liphistius* on mainland Asia lies west of the Mekong. As *Heptathela tonkinensis* (Bristowe) is known from northern Vietnam, presumably other *Heptathela* species can be found east of the Mekong in Laos and Cambodia too. Reports from these countries are awaited with anticipation.

Cyclocosmia has a disjunct trans-Pacific distribution, occurring in the Indochinese Subregion (Thailand, southeastern China) and in the Nearctic Region (southern USA, Mexico) (GERTSCH & PLATNICK 1975). Another disjunction is apparent for *Phyxioschema*: *Phyxioschema suthepium* is present in Thailand, *P. raddei* Simon in Palearctic Turkmenistan and Afghanistan (RAVEN & SCHWENDINGER 1989). However, since both species are small and inconspicuous, they may have been overlooked in the intervening area.

Chilobrachys is widely distributed in the Indian (Sri Lanka, India) and Indochinese Subregion (Burma, Thailand, China, Vietnam). *Damarchus* is found almost all over the Oriental Region, from India to Sumatra. *Calommata* and *Macrothele* range over parts of the Oriental, southern Palearctic and Ethiopian regions. *Atypus* is Holarctic and Oriental in distribution. The species in Thailand show relations to southern (*A. dorsualis* closest to *A. javanus* Thorell from Java and Sumatra) and northeastern taxa (*A. suthepicus* closest to *A. suiningensis* Zhang from southeastern China and to *A. karschi* Dönitz from Japan and Taiwan; SCHWENDINGER 1990*c*). *Idiops* is distributed in tropical and subtropical Asia, Africa and America. However, species outside America possibly have to be placed in the genus *Titanidiops*, now in synonymy (WUNDERLICH 1991: 280). Though distributed around the globe, *Atypus* and *Idiops* do not occur east of the Wallace Line. Only few genera present in Thailand range across this zoogeographical landmark: *Conothele* and *Phlogiellus* are distributed from China and Burma to Australia.

As can be expected, the fauna of orthognathous spiders in Thailand is composed of mostly Oriental and southern Palearctic forms. Few genera are also found in the Ethiopian (*Calommata*, *Macrothele*, *Idiops*), the Australian (*Conothele*, *Phlogiellus*) and the Nearctic Region (*Atypus*, *Cyclocosmia*). In contrast to results on linyphiid spiders by MILLIDGE (1995), very little congruence is evident between the mygalomorph spiders (the more ancient of both taxa) of Thailand and the Neotropic Region. Only *Idiops* (*Idiops* - *Titanidiops*?) is present in both areas. MILLIDGE's (1995) hypothesis that a part of Southeast Asia was attached or adjacent to South America before the break-up of Gondwanaland, therefore, cannot be supported.

Zoogeographical connections with the Nearctic and the Australian Region are interpreted as a result of vicariance and dispersal. The essentially continuous Australasian distribution of *Conothele* and *Phlogiellus* is probably due to a southward migration via land-bridges and stepping stones in the Malayan Archipelago during periods of lowered sea level in the Pleistocene (cf. MAIN 1981*a*, *b*). *Phlogiellus* (as also the widely distributed *Selenocosmia*, which ranges from India to Australia) has relatively good powers of dispersal. *Conothele*, which builds trapdoor nests in depressions on tree trunks and burrows in dead wood, may have rafted on logs or dispersed on gossamer (MAIN 1957).

Three cases of trans-continental relationships are remarkable. The trans-Pacific disjunction of *Cyclocosmia* is presumably a relict of a Palearctic or Asiamerican (PLATNICK 1976) distribution in the Mesozoic. *Prothemenops* and *Angka* from Thailand are taxonomically closer to the Australian Aganippini and *Kiama* respectively than to any mygalomorph spiders from Asia. They presumably are vicariant sister groups, each pair originating from a common ancestor in the pre-Jurassic, when parts of Southeast Asia were attached to northeastern Gondwanaland (AUDLEY-CHARLES 1987).

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First fossil mesothele spider, from the Carboniferous of France

Paul Antony SELDEN
Department of Earth Sciences
University of Manchester
Manchester M13 9PL, United Kingdom.

First fossil mesothele spider, from the Carboniferous of France. - *Eothele montceauensis* n. gen., n. sp., is described from two specimens from the Upper Carboniferous (Stephanian) of Montceau-les-Mines, France, as the first fossil and oldest known mesothele spider. In addition to the plesiomorphies characteristic of mesotheles, the holotype of *Eothele* preserves one mesothele synapomorphy (deep, narrow sternum) and at least one autapomorphy of the genus (biserially dentate chelicerae). The fossil is evidence that both mesotheles and opisthotheles were present in the Carboniferous period.

Key-words: Araneae - Carboniferous - fossil - France - Mesothelae - palaeontology - phylogeny.

INTRODUCTION

The south-east Asian spiders *Liphistius* Schiödte, 1849, and *Heptathela* Kishida, 1923, constitute the suborder Mesothelae which is sister group to Opisthothelae to which all other extant spiders belong (Platnick & Gertsch 1976). Mesotheles exhibit the most primitive character states of all living spiders, including segmented opisthosoma, eight spinnerets (seven in *Heptathela*) in a medioventral position on the opisthosoma, and absence of spinneret tartipores (Selden *et al.* 1991). Autapomorphies of Mesothelae include: modified trichobothria, invaginated fourth coxae, pseudosegmented lateral spinnerets, tibial spurs, and deep and narrow sternum (Platnick & Goloboff 1985; Raven 1985). As primitive spiders, it would be expected that mesotheles should appear early in the fossil record and, indeed, many Carboniferous spiders were referred to this suborder (as Liphistiina) in the Treatise (Petrunkevitch 1955). However, re-examination of all available types of

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Carboniferous spiders for a monograph of the group (in preparation) has revealed that none shows autapomorphic characters of Mesothelae. Of the eleven genera included in Mesothelae in Petrunkevitch (1955), one (*Palaeocteniza*) has been shown not to be a spider (Selden *et al.* 1991), and the remainder can be referred to Araneae only on the absence of autapomorphies of related orders (they have the general appearance of spiders, show segmented opisthosomae, but supposed spinnerets are artefacts).

In the last few years, some new specimens of fossil arachnids have been discovered at the locality known as Montceau-les-Mines in the Massif Central region of France. Among them, two specimens of Araneae have been identified, one of which is quite remarkable in that spinnerets are clearly preserved. The two specimens were mentioned briefly by Selden (1996) and are described fully here. The fossils are presumed to belong to the same species of spider, which shares most of the plesiomorphic character states of modern mesotheles, and a single synapomorphy: narrow, deep sternum (Raven 1985). At least one autapomorphy (biserial cheliceral dentition) separates the fossil species from living mesotheles. The fossil is evidence that both mesotheles and opisthotheles were present in the Carboniferous period.

MATERIAL AND METHODS

A number of fossil arachnids, including opilionids and trigonotarbids, are known from the Carboniferous (Stephanian) locality of Montceau-les-Mines in the Massif Central region of France, most of which are yet to be described. A recent review of the geology and palaeontology of the locality is given in Heyler & Poplin (1994). In that book, two photographs (p. 165) are labelled as spiders; the left photograph could be of a spider, but the specimen needs further development (specimen n° 5190/1), the other (specimen n° 6165) is not a spider. The specimen described here with the prefix 'In' is housed in the Department of Palaeontology, British Museum (Natural History), London, the other specimen is deposited in the Museum d'Histoire Naturelle, Autun, France. The fossils are external moulds in clay ironstone nodules.

THE MONTCEAU-LES-MINES SPIDER

Order ARANEAE Clerck, 1757
Suborder Mesothelae Pocock, 1892
Eothele n. gen.

Etymology: Greek *eos*, the dawn, and *thele*, a nipple; combining reference to the early age of the spider and the common suffix for mesotheles and mygalomorphs.

Diagnosis: mesothele spider with biserially dentate chelicerae (≥ 5 teeth on promargin, ≥ 3 teeth on retromargin); at least 6 spinnerets in two rows (4, 2) on ventral surface of opisthosoma, not bunched together at posterior margin of second operculum.

Type and only species: *Eothele montceauensis* n. sp., described below.

Eothele montceauensis n. sp. (Figs 1–4)

Etymology: after Montceau-les-Mines, France, the provenance of the fossils.

Diagnosis: as for the genus.

Horizon & locality: Carboniferous (Stephanian), Montceau-les-Mines, Massif Central, France.

Type material: Holotype specimen, numbers 51961 (part) and 51962 (counterpart), housed in Museum d'Histoire Naturelle, Autun, France. Second specimen (not to be considered a paratype), In 62050 (part) and In 62050a (counterpart), same locality, British Museum (Natural History), London.

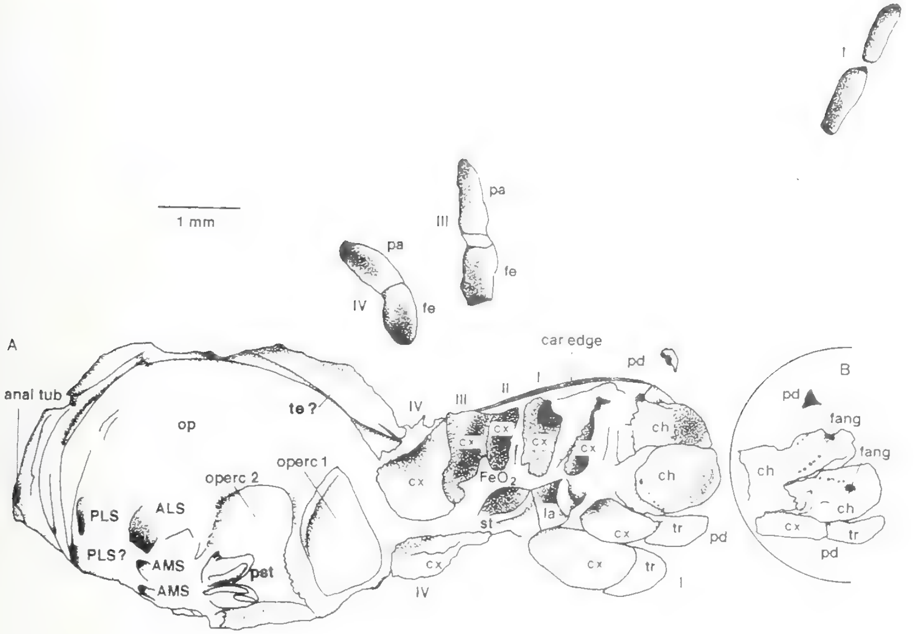
Description of specimen 51961/2

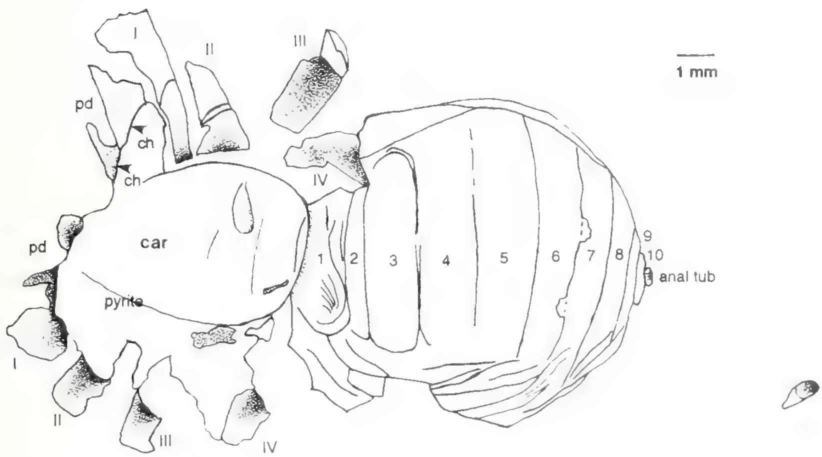
The specimen consists of ventrolateral (part: specimen n° 51961) and dorsolateral (counterpart: specimen n° 51962) external moulds in a nodule. The part shows most detail (Figs 1,3), including most of the prosoma and opisthosoma. The counterpart preserves only a few holes where legs disappear into the matrix, and vague details of the carapace. The dorsolateral mould of the opisthosoma, which should be on the counterpart, is missing; it is possible that a sliver of matrix preserving the mould was lost on splitting the nodule. It is impossible to tell whether the fossil represents a male, female or juvenile specimen.

The morphology of the specimen is essentially clear on the part (Figs 1,3). The opisthosoma has been compressed, the prosoma less so. The inflated shape of the opisthosoma indicates that this specimen represents a dead animal rather than a moult because in spider moults the opisthosoma is shrivelled. The coxae of all prosomal appendages on the left side, both chelicerae, and coxae of the right pedipalp and leg I are clearly displayed. The prosoma is tilted to the left, so that the coxae of legs II to IV are not seen on the part. Between the coxae, the labium and the left two-thirds of the sternum can be seen. The edge of the sternum drops steeply then flattens sharply to the right. The external mould of the labium disappears beneath the internal mould of the mouth. Labium and sternum are about the same width. Tilting the specimen reveals the external mould of the chelicerae (inset B on Fig. 3). Each of these shows a large pit distally which represents the external mould of the fang, and a line of holes (5 can be seen on each chelicera) running proximally from the fang represents the promarginal line of teeth. On the left chelicera, a line of three holes on the left side marks a retromarginal tooth row, but this cannot be matched on the right chelicera. Beyond the lateral edges of the coxae is a narrow groove which marks the external mould of the edge of the carapace. Beyond this there are some holes, the posterior two of which were developed further. These holes represent the external moulds of prosomal appendages. The posterior two represent the femora and patella of legs III and IV; looking inside the mould of femur IV, two grooves can be seen, which were ridges on the inferior surface of the femur in life. Two elongate holes about 4 mm from the edge of the carapace are two distal podomeres of leg I (presumably leg II is entirely hidden within the matrix). A small hole close to the carapace edge is the

Figs 1 & 2

Eothele montceauensis n. gen., n. sp., Carboniferous (Stephanian), Montceau-les-Mines, France. Fig. 1 (upper): holotype, specimen 51961 (part); see Fig. 3 for explanation; x13. Fig. 2 (lower): additional specimen, In 62050 (part); see Fig. 4 for explanation; x6.





FIGS 3 & 4. *Eothele montceauensis* n. gen., n. sp., Carboniferous (Stephanian), Montceau-les-Mines, France. Fig. 3 (upper): holotype, specimen 51961 (part); A: right dorsolateral view of external mould of left ventrolateral; B: dorsal view of external mould of chelicerae showing fangs (holes disappearing into matrix) and tooth rows. Fig. 4 (lower): additional specimen, In 62050 (part), ventral view of external mould of dorsal. Legend for Figs 3 & 4: 1–10—opisthosomal tergite numbers, ALS—anterior lateral spinneret, AMS—anterior median spinneret, anal tub—anal tubercle, car—carapace, ch—chelicera, cx—coxa, fe—femur, I–IV—walking legs I–IV, la—labium, operc—book-lung operculum, op—opisthosoma, pa—patella, pd—pedipalp, PLS—posterior lateral spinneret, pst—paired structure, st—sternum, te—tergite, tr—trochanter.

mould of the left pedipalp; it lines up with a hole in the counterpart. The region of leg II to IV coxae is obscure; whilst some shapes can be made out, it is not obvious whether they represent the mesial edges of coxae or also include any additional sternites. The counterpart shows small holes which represent the femora of right legs IV, III and II. The external mould of femur I is clearly displayed, disappearing into the matrix, with the mould of the pedipalp femur in front. On the other side, the left pedipalp femur mould can be seen. If the specimen is tilted so that the area to the mesial side of the legs is flat, a symmetrical shape can be discerned, which represents the external mould of the anterior part of the carapace in the eye region. Some circular structures can be made out, but they are rather faint. No trace of the opisthosoma is seen on the counterpart.

The opisthosoma on the part is beautifully displayed, and larger than the prosoma. It shows, on the right side in the anterior half, two sternites (book-lung opercula). The left lateral and median parts of these are flat, but their right sides bend upwards and are folded at the edge of the specimen. The anterior sternite has a straight anterior edge, the lateral edge runs obliquely inwards then curves to form the posterior edge which parallels the anterior. The second operculum is slightly larger than the first, and has procurved anterior and posterior margins and rounded lateral margins. In a posteromedial position on the second operculum is a pair of subelliptical areas of internal mould, which represent paired internal sac-like structures lying above the second operculum and opening to the medial part of its posterior border in life. These were initially interpreted as paired receptacula of the female vulva, but in living spiders the genitalia are on the second opisthosomal somite; the second operculum is on the third opisthosomal somite. In the fossil, the book-lung opercula are interpreted as belonging to somites 2 and 3, as in *Liphistius*. These sac-like structures are most similar to the supposed tracheal organs of the mesothele *Heptathela* (YOSHIKURA 1954); they do not occur in *Liphistius*, but may be homologous to the eversible sacs in Amblypygi (KAESTNER 1968).

Posterior to the second operculum are three holes extending into the matrix, the leftmost being larger than the other two, which are about the same size. These are interpreted as external moulds of the left anterior lateral spinneret (ALS) and the anterior median spinneret pair (AMS). The right ALS is presumed lost among the folds of the right part of the opisthosoma in the fossil. Posterior to the anterior spinneret moulds are two more holes which represent posterior spinnerets. The anterior spinnerets are in the mesothele conformation. Four posterior spinnerets (smaller posterior median, PMS; larger posterior lateral, PLS) are present in all spiders, except when the PMS are missing (some specialized mygalomorphs and araneomorphs), or a single PMS is present (the mesothele *Heptathela*). The fossil posterior spinnerets could represent left PLS and left PMS, PLS only, PMS only, or left PLS and single PMS. Evidence favouring a single pair of posterior spinnerets is a) the holes are approximately the same size, and b) an imaginary midventral line running from between the paired median structures of the second operculum, between the AMS, to the anal tubercle, parallel to the edge of the opisthosoma would pass between the two holes, but a line passing to the right of the right-most hole would have to follow a

dog-leg course to reach the anal tubercle. Since the PMS are usually smaller than the PLS, or lost (Marples, 1967), the posterior spinnerets present in the fossil, which are relatively large, are most probably PLS.

The left side of the opisthosoma bears a number of random, irregular nodules. Beyond these are some curved folds which approximately parallel the edge of the opisthosoma. No tergites are visible. This may be because any tergites which were present were confined to the dorsal side of the opisthosoma. On the part, only ventral and lateral sides are visible, the counterpart preserves no fragment of the opisthosoma. On the left lateral side of the opisthosoma, which would have been the anterior part of the dorsolateral in life, one fold is larger and more robust than the rest (which suggests it was composed of tougher cuticle in life) and extends for about 1/3 of the length of the opisthosoma. In front of this structure is a smaller, yet similarly robust fold. The possibility that the larger structure could represent a dorsal scutum was considered, but further thought and study of some other well-preserved Carboniferous spiders has led to the conclusion that this specimen probably did bear dorsal tergites. These, like the carapace, would have been preserved on the counterpart. However, like the carapace, which is preserved on the part as a thin groove—the external mould of the edge of the carapace, the opisthosomal tergites have also left their mark on the part as a narrow external mould. I suggest that during compression of the fossil, the dorsal tergites remained fairly rigid compared to the flexible cuticle of the sides of the opisthosoma. Where there were no adjacent tergites, such as over most of the preserved left and posterior parts of the opisthosoma, this flexible cuticle is expressed as simple folds on the external mould. On the left anterolateral side, however, the second and following tergites above compressed the flexible cuticle onto the sediment to produce an apparently robust fold. In front of this, the short first opisthosomal tergite has produced a similar fold. Segmentation is not apparent because it is the lateral cuticle which formed the floor of the crevice, not the tergites themselves.

Description of specimen In 62050

The specimen (Figs 2,4) consists of dorsal (part: specimen n° 62050) and ventral (counterpart: specimen n° 62050a) external moulds in a nodule. The part shows most detail (Figs 2,4), including much of the prosoma and dorsal opisthosoma. The counterpart preserves only a few holes where legs disappear into the matrix, and some parts of the book-lung opercula on the ventral opisthosoma. The ventral mould of the prosoma, which should be on the counterpart, is missing because a sliver of matrix preserving the mould was lost on splitting the nodule. In places, details are obscured by a thin veneer of pyrite and calcite (?) crystals; kaolinite is rare, and occurs mainly as a cast of thin tubes (possibly distal podomeres) towards the edge of the nodule. The specimen is strongly three-dimensional, its shape no doubt reflects the original shape of the animal. There is slight distortion in that the prosoma is rotated slightly in relation to the opisthosoma, so that in the chelicerae and other prosomal appendages appear to lie off the midline of the carapace when the specimen is lying with the opisthosoma symmetrical to view. By rotating the specimen, the

carapace and appendages can be positioned so that they are almost symmetrical, when the opisthosoma is not. The slight displacement of the chelicerae is then explained by a little compaction of the sediment prior to the formation of the nodule. It is impossible to tell whether the fossil represents a male, female or juvenile specimen.

The carapace is preserved as an external mould, but is obscured, especially anteriorly, by mineralisation. It is roughly oval in shape, widest at or behind its midlength, but the anterior border is not visible in the specimen, being covered by matrix surrounding the anterior appendages. The posterior margin of the carapace is approximately straight, with a slightly recurved submarginal line; it is about half the width of the carapace at its widest. The chelicerae are preserved as two holes, separated by a mineralised sheet of rock matrix, anterior to the carapace and disappearing into the nodule anteriorly. No details can be discerned. The pedipalps and walking legs are preserved only as external moulds of parts of the proximal podomeres. Holes descending into the matrix around the carapace represent the upwardly rising femora. A few thin holes well beyond the main body of the fossil may represent distal podomeres descending again.

The opisthosoma is represented on the part by a sub-hemispherical hole: the external mould of its three-dimensional form. The inflated shape of the opisthosoma indicates that this specimen represents a dead animal rather than a moult because in spider moults the opisthosoma is shrivelled. Lateral parts of the opisthosoma, especially anteriorly, are distinctively longitudinally wrinkled. (Similar wrinkling occurs on the soft parts of the opisthosoma of *Liphistius*). The dorsal surface of the opisthosoma consists of a series of tergites, at least eight can be counted. The more anterior tergites are longer (sag.) than the posterior, but telescoping of the opisthosoma posteriorly conceals their true lengths. Another tergite (1) may be present between the most anterior well-defined tergite and the carapace, but wrinkling on the left side of the specimen (right side of the animal) suggests that this area could consist of soft cuticle. The tergites have fairly straight anterior and posterior margins and, where visible, their lateral margins appear to be rounded. At the posterior end of the opisthosoma, just posterior to a possible microtergite (10), is a hole which represents the external mould of the anal tubercle. On the counterpart (specimen nº 62050a), the external mould of a small part of the left side of the opisthosoma can be seen. This region is characteristically transversely wrinkled. Two transverse grooves may represent the posterior margins of book-lung opercula 1 and 2.

DISCUSSION

It is tempting to assume that the two Montceau specimens belong to the same species, but the morphological evidence neither proves nor disproves this supposition. Features shown by the Autun specimen are not preserved on the London specimen, and vice versa. However, the two fossils are approximately the same size and occur in the same locality and lithology. At other Upper Carboniferous localities yielding arachnids in concretions, such as Coseley (UK) and Nýřany (Czech Republic), diversity within orders is low, and similar specimens have usually been assigned to

the same species (this is true for the Nýřany 'spiders', but is not yet published). All ten specimens of the earliest mygalomorph, *Rosamygale grauvogeli* Selden & Gall, 1992, found at the Triassic locality in the Vosges, France, belonged to one species. For these reasons, the two Montceau-les-Mines specimens will be assumed to be conspecific, until further evidence (in the form of more specimens) might prove otherwise.

Since the two specimens reveal essentially different aspects of the morphology of the Montceau spider, a reasonable reconstruction of the living animal can be built up. The fossil animal is clearly a spider because of the presence of spinnerets (at least, appendages are present in the position in which spinnerets occur in living spiders, and no other arachnid has such appendages in this position; spinnerets are taken to indicate the presence of opisthosomal silk glands) combined with a pedicel, an essentially flexible opisthosoma with the tergites 'floating' in softer cuticle, general appearance of the carapace and sternum, and lack of autapomorphies of other arachnid groups. Some autapomorphies of spiders, naked fang and cheliceral poison gland for example (SELDEN *et al.* 1991), cannot be seen.

There are few described autapomorphies of mesotheles (PLATNICK & GERTSCH 1976; PLATNICK & GOLOBOFF 1985). One of these relates to chromosome numbers so cannot be confirmed in fossils; the other characters (trichobothrial bases, invaginations of fourth coxae, multisegmented lateral spinnerets, tibial spurs) are morphological, but none of them can be seen in the Montceau fossils. An additional apomorphy of mesotheles was suggested by RAVEN (1985): a deep and narrow sternum. He contended that the presence of a sternum is an autapomorphy of Araneae (it is absent or very small in Amblypygi and most other arachnids), and that in Opisthothelae it is wide and low (an autapomorphy of that group). SELDEN *et al.* (1991) considered the presence of a sternum to be plesiomorphic within the Tetrapulmonata (Trigonotarbida have one also), but this does not alter the apomorphic state of the sternum in the mesotheles and opisthotheles. The characters of dorsal opisthosomal tergites, two ventral opercula (covering the two pairs of book-lungs), orthognath chelicerae, and AMS fully developed, are all indicative of Mesothelae, but are plesiomorphies. The deep, narrow sternum of the Montceau spider is a character shared with modern mesotheles. If the paired structures above the second operculum in the fossil are not homologous with amblypygid eversible sacs then this character would be a synapomorphy for *Heptathela* and *Eothele* n. gen. (Fig. 5A). The spinneret pairs in *Eothele* are widely spaced between the second operculum and the anal tubercle, not bunched together just behind the second operculum as in modern mesotheles nor close to the anal tubercle as in Opisthothelae. The position of the spinnerets in *Eothele* could reflect the start of their rearward movement towards the opisthothelate condition, or a more ancestral arrangement prior to the bunching of the spinnerets close to the second operculum as seen in *Liphistius*. If the posterior spinnerets in *Eothele* are really PLS, then it would represent a new configuration for Araneae, an advance over the *Heptathela* condition (with a single PMS), and an autapomorphy for the fossil species. Another feature which separates *Eothele* from modern mesotheles is the presence in the fossil of two rows of teeth on the chelicera (Fig. 3,B); only a

promarginal row is present in living forms (ABRAHAM 1929; BRISTOWE 1932). Biserially dentate chelicerae are special adaptations which have evolved in a number of spider groups. For example, RAVEN (1985) considered the biserial condition to be apomorphic in ctenizoid mygalomorphs and some related idiopids and cyrtaucheniids. Amblypygids and the Devonian spider *Attercopus* have uniserially dentate chelicerae (SELDEN *et al.* 1991).

FOSSILS AND PHYLOGENY

Much has been written concerning the value of fossils in piecing together the relationships between animal groups (see a recent review by SMITH, 1994). It has become clear in the last twenty years or so that fossils must play a secondary role in establishing phylogenetic relationships, but an important one in providing raw data and, in some cases, resolving conflicting cladograms. Some authors have attempted to use stratigraphic data in cladistic analyses (e.g. FISHER 1992, 1994; WAGNER 1995) but such analyses need to be executed with caution. The fossil record of arachnids is still so sparse that the discovery of single specimens can make major alterations to the known fossil record. The new spider described here is a case in point: it is the first known fossil mesothele, thus extending the record of this group from 0 years to 290 million years. The unique contribution fossils can make is in the construction of evolutionary trees, the next logical step in understanding the phylogenetic history of an animal group after the construction of cladograms. It has been shown (for example by SMITH 1994, chapter 6) that stratigraphic data can be combined with a robust cladogram to produce an estimate of the evolutionary tree of a group which minimises stratigraphic gaps. A normal result of this process is the production of range extensions and ghost lineages; these are predictions made by the data. Note that fossil data provides minimum estimates for the dates of divergence of clades.

Possession of many character states which indicate that the Montceau spider is plesiomorphic with respect to Opisthothelae, and one character state (sternum narrow and deep) which is an autapomorphy of Mesothelae, confirm that the Montceau spider belongs in Mesothelae. The fossil species cannot be ancestral to any modern mesothele because of at least one autapomorphy (biserially dentate chelicera). Therefore, the fossil is the oldest record of a mesothele. Furthermore, since Opisthothelae (Mygalomorphae + Araneomorphae) is the sister clade to Mesothelae, it must have originated sometime prior to the age of the fossil. Fig. 5 illustrates these relationships.

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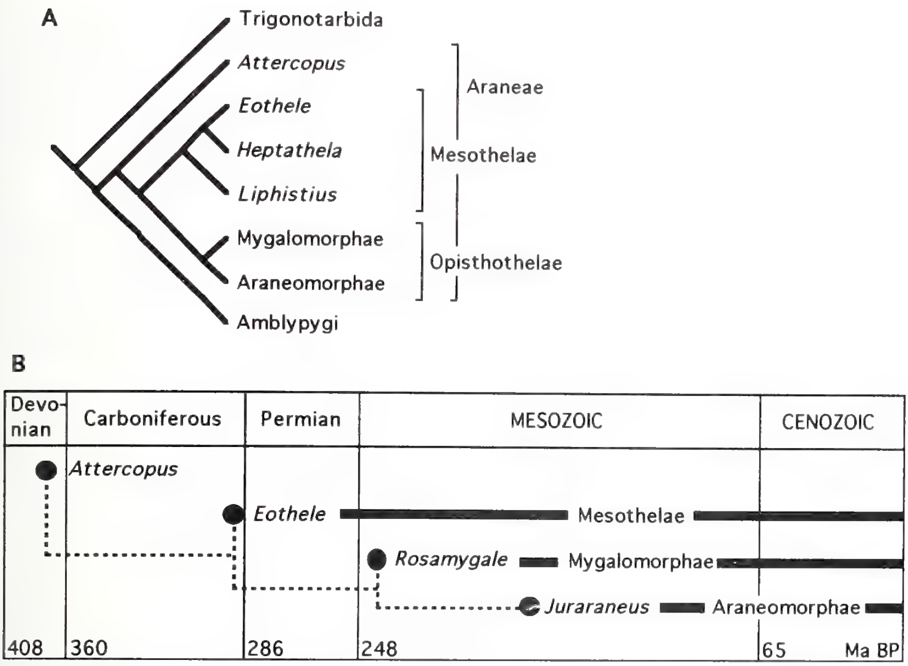

FIG. 5

A: cladogram of relationships among Trigonotarbida, Amblypygi, and selected spider taxa. The Montceau spider *Eothele* is shown as sister to *Heptathela* because tracheal sacs are absent in *Liphistius* and on the assumption that PMS are lost in *Eothele*. B: Evolutionary tree showing relationships between spider suborders (emphasising the earliest fossil members) and *Attercopus*; solid black lines are known ranges (fossil record of Mesothelae consists solely of *Eothele*; other suborders have better fossil records); horizontal dashed lines are ghost lineages for (Mesothelae + Opisthothelae) and (Mygalomorphae + Araneomorphae) and range extension for Araneomorphae; vertical dashed lines show hypothesized relationships.

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Species composition and community structure of peruvian rainforest spiders: A case study from a seasonally inundated forest along the Samiria river

Diana SILVA
Dept. Entomology, Comstock Hall, Cornell University
Ithaca NY 14853, USA

Species composition and community structure of peruvian rainforest spiders: A case study from a seasonally inundated forest along the Samiria river. - Field work was carried out along the Samiria river, in the Pacaya-Samiria National Reserve, northeastern Peru (Loreto), at the end of the rainy season, May-June 1990. More than a thousand morphospecies belonging to at least 39 families of spiders were collected from various canopy and understory microhabitats by using a combination of fogging and conventional sampling techniques. Over half of the species belong to only three families: Salticidae (19%), Theridiidae (16%), and Araneidae (18%). Diversity and abundance for the former two families were higher in the canopy, while for the last one they were higher in the understory. The highest number of species (151) was found in one of the most heterogeneous canopy microhabitats. A few species accounted for 1-3 % of the adult spiders, the great majority did not reach 0.5 % of the total number of adults collected (5,895 indiv.). The two most complex categories of microhabitats from the canopy and the understory strata appeared to be moderately distinct, 59% of species were present in only one or the other. However, single sets of microhabitats from both strata exhibited a narrow spider species overlap, on average, 89% of complementarity.

Key-words: canopy-understory-spiders-Neotropics-fogging-biodiversity

INTRODUCTION

Trees provide a suite of useful microhabitats for the study of animal communities. Individuals in the arboreal community are all more or less trophically interlinked, and they are unified in their dependence on the tree. Trees are also structurally complex, providing potentially great niche diversification for their inhabitants. These attributes help account for the extraordinary species richness of arboreal communities (Moran & Southwood 1982; Farrel & Erwin 1988; Basset & Arthington 1992).

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In the last 15 years, it has been shown that tropical tree canopies are extremely rich in insects and other arthropod species (ERWIN 1983, ADIS *et al.* 1984; STORK 1991); recent studies are also providing new information about species richness, abundance and community structure of tropical spiders (BASSET 1991; GUILBERT *et al.* 1995; HÖFER *et al.* 1994; RUSSELL-SMITH & STORK 1994, 1995). It appears from them that microhabitat qualities are playing an important role in the distribution of the canopy spider species.

Physical qualities of particular microhabitats allow spiders to finely partition available space into specific, more narrowly defined niches. This in turn has an important effect on the species richness and abundance of spiders and although most species exhibit very narrow, patchy distributions, spiders as a whole comprise one of the most conspicuous and diverse groups of terrestrial invertebrates (BARNES 1953; DUFFEY 1978, 1993; HÖFER 1990; CODDINGTON & LEVI 1991; MASON 1992; NENTWIG 1993).

Based on semi-quantitative data, this paper attempts to provide comparative information on microhabitat differences in species richness, species composition, and community organization of the spiders from the canopy and understory of an Amazonian forest as well as to contribute towards a better understanding of spider species diversity.

MATERIALS AND METHODS

STUDY SITE. Samiria river is a blackwater river located in the Pacaya-Samiria National Reserve, northeastern Peru (74°21'-75°28'W/04°39'-05°07'S), 80-100 m elevation. Despite vast floodings during the rainy season, November to April, the forests along the Samiria river are highly diverse, and are characterized by buttressed trees up to 45-55 m high, forming an almost closed canopy with numerous epiphytes and vines. A detailed description of the study area is being prepared (Erwin, pers. comm.).

SAMPLING TECHNIQUES. During four weeks between May and June 1990, various microhabitats from the canopy (above 10 m high) and the understory (0-10 m high) strata were chosen along the Samiria river according to their distinctive architecture. These microhabitats fell into six main categories: 1) dry leaves hanging in the undercanopy, 2) vines mixed with dry leaves of trees, 3) vines, 4) palms, 5) epiphytes, and 6) one or more huge trees and associated vines plus epiphytes, e.g., more "complex" habitats (Table 1).

The microhabitats in the canopy and the understory were sampled by using a fogging technique (ERWIN 1990). Each fogging consisted of sufficient biodegradable resmythrin insecticide to fog the entire selected microhabitat. One to six 2-m2 plastic sheets were placed under the selected microhabitats, and all the arthropods which fell onto them during the 2 hr period after fogging were collected. The canopy fogging (at least 20 hours of collection) took place at dawn, while the fogging of the understory microhabitats (at least 78 hours) took place at different hours of the day depending on wind conditions.

Spiders from the understory were also collected by a time-based search of at least 84 hours of looking up and down (CODDINGTON *et al.* 1991), and by beating lower tree branches (at least 1 hour), and sweeping herbaceous vegetation (2 hours).

DATA ANALYSIS. The criterion used to determine species richness was the number of species present in each sample (SOUTHWOOD *et al.* 1982). The degree of complementarity (distinctness), "the proportion of all species in two sites that occurs in only one or the other of them," was measured by the formula suggested by COLWELL & CODDINGTON (1994:112): Cjk = Ujk/Sjk [# species unique to either site)/(species richness for both sites combined)], where Ujk = Sj + Sk - 2Vjk, and Sjk = Sj + Sk - Vjk; S = # species in sites j and k, and Vjk = # species shared by sites j and k.

According to this formula, the fauna of two sites will be completely distinct when C= 100%. Species density was summarized by a 3-point abundance scale: rare= 1-4; common= 5-15; dominant= over 15 individuals. All spiders were counted but only the adults were sorted to morphospecies. Juveniles and voucher specimens were deposited in the Natural History Museum of Lima, Peru.

Patterns of spider community organization were analyzed by assigning each family to one of four functional groups which were defined by differences in prey-capture strategies (RIECHERT & HARP 1987; UETZ 1992). Orb weavers and sheet-line weavers rely on vibratory cues through silk webs to detect their prey; ambush predators do not use capture webs and remain stationary for long periods of time waiting for prey; while cursorial hunters move more or less constantly searching for prey. It must be pointed out that this is just a way to facilitate future comparisons, because within any guild there is a great deal of variation in prey-capture strategies, and a much greater amount of work is required to do a more precise and meaningful partitioning of functional groups.

RESULTS

Microhabitat differences of abundance and species richness. In terms of abundance, about half the total number of spiders collected by fogging were recorded from the "complex" microhabitats (42%) alone, followed by dry leaves (24%). When only the adults (38% of the total) were considered, the spiders were about equally distributed across four samples, with the "complex" microhabitats as the most abundant (23%), followed by dry leaves (19%), vines (17%), and epiphytes (16%) (Tables 1-2).

Species richness varied markedly across microhabitats. However, comparisons of single samples showed the richest habitats were those with mixed vegetation (20%), vines (20%), dry leaves (18%), and epiphytes (16%) (Table 1).

Community organization. The most abundant functional groups were the cursorial hunters (30%) and the sheet-line weavers (29%). The orb weavers (22%) and the ambush spiders (19%) were also important components of this community (Table 2).

TABLE 1

Microhabitats, abundance and number of spider species from the Samiria forest. Ca= canopy, Un= understory. Each of the microhabitats represent a single sample.

MICROHABITAT	JUVENILES		FEMALES		MALES		SPECIES	
	Ca	Un	Ca	Un	Ca	Un	Ca	Un
DRY LEAVES (DRL)								
Dry leaves clumped on vegetation at 1 m		36		10		13		19
Dry leaves scattered in undercanopy at 2 m		116		41		32		38
Dry leaves scattered in undercanopy at 2 m		28		12		8		15
Dry leaves scattered in undercanopy at 3 m		70		12		10		16
Dry leaves scattered in undercanopy at 3 m		82		21		22		32
Dry leaves in undercanopy at 3 m		175		42		41		51
Dry leaves in tree		113		44		56		44
Dry leaves in tree		159		88		52		66
Dry leaves in tree		36		15		10		19
Dry leaves in tree		82		16		26		28
Dry leaves hanging in undercanopy		920		141		143		137
DRY LEAVES AND VINES (DLV)								
Dry leaves of vine under dense canopy*		33		11		7		15
Dry leaves of vine under dense canopy		47		21		16		19
Dry leaves and vines at 5 m		24		27		22		32
VINES (VIN)								
Lethycidacea plus vines, nr. river (fog. 20 m up)	599		189		159		146	
Dead tree stump with leafy vines		168		52		56		55
Tree with vines		59		41		31		48
PALMS								
Scheelea palm surface, shady (PAL)		122		54		37		48
Scheelea palms (4) and understory leaves (PAU)		147		35		31		35
Scheelea palms with epiphytes at 4 m (PAE)		159		91		73		66
Dry hanging leaves of *Mauritia flexuosa* (MAU)**		62		50		53		41
MAU with vines at 5m (MAU)**		118		31		26		22
Dry hanging leaves of *Mauritia flexuosa* (MAU)**		146		33		26		42
EPIPHYTES (EPI)								
Ficus plus epiphytes (fog. 40 m up)	458		123		114		119	
Large bromeliads on side of tree at 2 m		279		33		10		25
Bromeliads in *Ficus* *		14		10		5		11
COMPLEX ARCHITECTURE (COM)								
Big tree with vines and epiphytes*** (FOG 1 TLE-May)	336		164		150		122	
Big tree with vines and epiphytes (FOG 1 TLE-June)	120		30		42		42	
3 huge trees with vines and epiphytes	777		195		210		146	
Leguminosae with vines and epiphytes	429		120		96		126	
Big tree with vines and epiphytes*** (FOG 2 TLE-May)	537		199		133		151	
Big tree with vines and epiphytes (FOG 2 TLE-June)	361		56		79		89	
Big tree with vines and epiphytes (FOG 3 TLE-June)	465		136		111		116	
Tree nr. Manguifera, dense canopy*	11		3		4		7	

* Rain drastically affected the time of collection (approx. 20 min.)
**Swamp forest outside the Samiria river (74°18'W/04°43'S)
*** The same tree was fogged a second time after three weeks, approx.

TABLE 2

Abundance of spider families collected by fogging canopy and understory microhabitats. DRL= dry leaves, DLV=dry leaves & vines, VIN= vines, EPI= epiphytes, COM= canopy mixed vegetation, PAL= *Scheelea palms*, PAU= palms & understory leaves, PAE=palms & epiphytes, MAU= *Mauritia* palms.

	DRL	DLV	VIN	EPI	COM	PAL	PAU	PAE	MAU	TOTAL (%)
ORB WEAVERS	137	13	84	65	252	1	8	7	37	604 (14.9)
Anapidae	1	0	1	12	-	-	-	-	-	14
Araneidae	85	9	67	35	181	1	4	4	16	402
Deinopidae	1	1	-	-	1	-	-	-	-	3
Mysmenidae	3	1	-	1	5	-	-	1	9	20
Tetragnathidae	4	1	3	2	7	-	1	1	-	19
Theridiosomatidae	33	-	6	12	47	-	2	1	8	109
Uloboridae	10	1	7	3	11	-	1	-	4	37
SHEET-LINE WEAVERS	269	39	127	108	498	47	18	50	58	1214 (30)
Dictynidae	1	-	-	-	6	-	-	-	-	7
Hahniidae	-	-	-	-	-	-	-	-	1	1
Linyphiidae	2	-	11	-	3	-	-	-	-	16
Ochyroceratidae	1	-	-	-	-	-	-	-	-	1
Pholcidae	21	18	16	9	61	11	3	7	21	167
Rhoicininae	-	-	1	2	9	-	-	-	-	12
Scytodidae	7	-	4	7	33	2	1	-	2	56
Theridiidae	237	21	95	90	386	34	14	43	34	954
AMBUSH PREDATORS (18.5)	170	18	100	44	333	14	5	29	38	751
Ctenidae	11	6	1	1	18	4	-	8	3	52
Hersiliidae	5	-	6	1	17	-	-	-	1	30
Heteropodidae	44	7	19	5	58	1	-	8	11	153
Mimetidae	7	-	5	9	20	-	-	2	7	50
Oxyopidae	2	-	1	1	26	-	-	-	1	31
Pisauridae	7	-	1	2	14	-	-	1	7	32
Selenopidae	-	-	-	-	4	-	-	-	-	4
Senoculidae	5	1	4	-	5	1	-	1	-	17
Thomisidae	88	4	62	25	171	8	5	9	8	380
Trechaleidae	1	-	1	-	-	-	-	-	-	2
CURSORIAL HUNTERS (36.6)	294	37	199	87	636	28	35	79	86	1481
Anyphaenidae	25	1	13	7	34	1	1	7	1	90
Aphantochilidae	3	-	13	-	13	-	1	1	2	33
Caponiidae	4	2	-	1	10	1	-	1	1	20
Clubionidae	1	4	-	4	-	-	-	-	-	9
Corinnidae	41	3	17	7	74	5	1	4	21	173
Gnaphosidae	10	-	14	2	34	-	-	3	2	65
Liocranidae	5	-	6	1	12	1	-	-	3	28
Lycosidae	-	-	1	-	-	-	-	-	-	1
Miturgidae	5	-	1	4	9	-	-	-	-	19
Oonopidae	74	13	70	19	142	18	27	21	10	394
Palpimanidae	-	-	-	-	-	-	-	-	1	1
Salticidae	125	14	63	42	307	2	5	42	44	644
Tetrablemmidae	-	-	1	-	-	-	-	-	-	1
Undetermined	1	-	-	-	1	-	-	-	1	3
ABUNDANCE (%)	870 (21.5)	107 (2.6)	510 (12.3)	304 (7.5)	1719 (42.4)	90 (2.2)	66 (1.6)	165 (4.1)	219 (5.4)	4050

In terms of abundance, families were not equitably distributed among the guilds (Tables 2-3). Salticidae (42%) were clearly dominant among cursorial spiders; while the most abundant orb weavers were Araneidae (65%). The great majority of sheet-line weavers were Theridiidae (79%), while among ambush predators the most abundant family was Thomisidae (39%).

When ranked according to the number of species (Table 3) cursorial spiders dominate all the microhabitats (36%), in part due to the high number of salticids. Orb weavers (28%), with Araneidae as the richest family, were also highly diverse. Sheet-line weavers ranked third (20%), with Theridiidae as the richest family. Among ambush predators (16%), Thomisidae was the most diverse family.

Species composition. A total of 5,895 adult spiders and 1,140 morphospecies, approx. 39 families, were recorded in this study (Table 3). A complete list is available on request. Over half of all adult spider species belong to only four families: Salticidae (220 species), Araneidae (207), Theridiidae (184) and Corinnidae (57).

The richest genera were *Eustala* (68 spp.), *Wagneriana* (25 spp.), *Micrathena* (14 spp.), and *Alpaida* (13 spp.) (Araneidae); *Dipoena* (46 spp.), and *Argyrodes* (28 spp.) (Theridiidae), *Encolpius* (17 spp.) (Salticidae); and *Tmarus* (11 spp.) (Thomisidae).

Despite the use of combined sampling techniques, some species, which accounted for 43% of the collection, were recorded from only one individual. Families like Hahniidae, Palpimanidae, and Tetrablemmidae were among the rarest taxa. Some other unidentified species with doubtful family placement were also very rare (Tables 2-3).

Species Dominance. Very few species, among them *Episinus erythrophthalmus* (2.5%), *Thwaitesia bracteata* (2.7%), and one unidentified oonopid (2.2 %), were collected in almost all microhabitats in high densities. Other species, like one unidentified Sparianthinae (1.8%), *Dipoena* nr. *nigra* (1.3%), *Tmarus* sp. (1.5%) and another oonopid (1.6%) were also abundant, either in the canopy and/or in the understory. Some other species such as aphantochilids, araneids, lycosids, theridiids, and thomisids, were commonly collected both in the canopy and the understory; however they accounted for less than 1 % of the total adult sample (Table 4). Species of *Ctenus*, *Corinna*, *Thaumasia*, and *Ancylometes*, were commonly found in the understory and, in terms of biomass, they were dominant in this stratum.

Complementarity. When all the microhabitats were pooled within their respective major categories and the categories compared, the proportion of species shared between pairs of samples (Table 5) was very low. The highest value (13 %) was found between dry leaves and complex microhabitats, which could be considered the most representative samples from the understory and canopy, respectively. These two microhabitats exhibited a moderate level of distinctness (C = 59%), while most other sets showed a higher level of complementarity, on average 88%.

When single microhabitats were compared (Table 6), the complementarity was stronger than when the microhabitats were combined, 89 % on average, indicating a very narrow overlap in spider species composition across them. Even the two samples from the same tree exhibited a strong species distinctness, averaging 88%.

TABLE 3

Abundance and species richness of spider families from the Samiria river. Singletons refer to the number of species with only one individual. FOG=fogging, LUD=looking up & down (day/night), BEA=beating, SWE=sweeping.

	FOG		LUDd		LUDn		BEA		SWE		Singletons	
	Ind.	Spp.	Ind.	Spp.	Ind.	Spp.	Ind.	Spp.	Ind.	Spp.	No.	%
ORB WEAVERS												
Anapidae	14	1	8	1					4	1	0	
Araneidae	402	139	164	63	205	80	6	6	6	6	98	47.3
Deinopidae	2	1	2	1	3	2					0	
Mysmenidae	20	7	33	11	14	8			2	2	5	45.4
Symphytognathidae			6	2							1	50.0
Tetragnathidae	19	9	50	7	28	14			4	3	18	56.2
Theridiosomatidae	112	18	45	18	14	8					14	45.2
Uloboridae	36	20	31	7	30	14					19	63.3
SHEET-LINE W.												
Dictynidae	7	1									0	
Hahniidae	1	1									1	100
Linyphiidae	16	4	11	5					10	3	4	40.0
Ochyroceratidae	1	1									1	100
Pholcidae	167	25	38	9	15	3	4	2			8	28.6
Rhoicininae	12	1	1	1							0	
Scytodidae	56	6	3	2	19	3					1	16.7
Theridiidae	954	137	275	49	161	55	6	4	11	6	80	43.5
AMBUSH P.												
Ctenidae	52	9	20	9	66	16					13	50.0
Hersiliidae	30	8	2	1	3	3					2	22.0
Heteropodidae	153	13	4	4	9	6					9	50.0
Mimetidae	50	15	2	2	29	14					7	30.0
Oxyopidae	31	16	2	2	4	3					9	53.0
Pisauridae	32	7	24	14	63	15					18	64.3
Selenopidae	4	2			1	1					0	
Senoculidae	17	2			2	2					0	
Thomisidae	397	45	10	7	10	5	3	3	1	1	20	40.8
Trechaleidae	2	2	7	3	5	2					3	50.0
CURSORIAL H.												
Anyphaenidae	90	40	8	7	22	10			2	1	20	41.7
Aphantochilidae	33	2			2	1					1	50.0
Caponiidae	20	1					1	1			0	
Clubionidae	9	3			1	1					1	33.3
Corinnidae	173	49	8	6	5	5			2	2	30	52.6
Gnaphosidae	65	12									3	25.0
Liocranidae	28	9									3	33.3
Lycosidae	1	1	60	11	19	3			7	3	4	33.3
Miturgidae	19	7			2	1					3	42.9
Oonopidae	394	30	4	5	1	1	3	3			11	35.5
Palpimanidae	1	1									1	100
Salticidae	644	195	65	32	23	17	9	6	2	2	105	47.7
Tetrablemmidae	1	1									1	100
Undetermined	3	3	1	1	1	1	1	1			6	100

TABLE 4

Relative abundance of the most common spider species from Samiria.

Species	Canopy	Understory	% Genus	% Family	% adults
ARANEIDAE					
Eustala (ARA140)	6	33	16.6	4.6	0.7
Eustala (ARA146)	32		13.6	3.8	0.5
APHANTOCHILIDAE					
Bucranium (APH1)	25	10	100	97	0.6
CAPONIIDAE					
Nops (CAP1)	9	12	100	100	0.4
CORINNIDAE					
Castianeira (COR33)		18	56.2	9.5	0.3
Corinna (COR4)	9	7	36.4	8.4	0.3
Trachelas (COR12)	6	22	62.2	14.7	0.5
CTENIDAE					
Ctenus (CTE12)		28	80	16.7	0.5
Gephyroctenus (CTE6)		25	62.5	14.9	0.4
HETEROPODIDAE					
Sparianthinae (HET2)	33	74	98	62.5	1.8
LYCOSIDAE 1	1	51		53.6	0.9
MIMETIDAE					
Ero (MIM10)	11	5	32.6	34.4	0.3
MYSMENIDAE					
Mysmenopsis (MYS2)	3	13	44.4	34.0	0.3
OONOPIDAE 10	82	45		31.6	2.2
OONOPIDAE 11	36	57		23.1	1.6
OONOPIDAE 6	39	16		13.7	0.9
OONOPIDAE 5	8	16		6.0	0.4
PISAURIDAE					
Paradossenus (PIS12)		19	100	13.6	0.3
Thaumasia (PIS14)	1	13	15.4	10.0	0.2
SALTICIDAE					
Acragras (SAL11)	2	19	62	2.8	0.4
TETRAGNATHIDAE					
Azilia (TET10)		26	92.8	27.1	0.4
THERIDIIDAE					
Dipoena (THD38)	29	15	10.7	3.3	0.7
Dipoena (THD57)	56	22	18.9	5.8	1.3
Dipoena (THD65)	29	26	13.3	4.1	0.9
Argyrodes (THD58)	4	16	17	1.5	0.3
Episinus (THD35)	53	94	79	38	2.5
Thwaitesia (THD2)	80	77	100	11.7	2.7
THERIDIOSOMATIDAE					
Naatlo (THS8)	20	9	44.6	18.0	0.5
Ogulnius (THS3)	11	12	68.8	19.9	0.5
THOMISIDAE					
Tmarus (THO1)	30	13	22.0	10.2	0.7
Tmarus (THO3)	29	13	21.5	10.0	0.7
Tmarus (THO13)	25	61	44.1	20.4	1.5
Acentroscelus (THO4)	41	5	55.4	10.9	0.8
Acentroscelus (THO23)	13	6	22.9	4.5	0.3
Strophius (THO24)	13	3	55.2	3.8	0.3

TABLE 5

Number of species shared between canopy and understory strata. The values of relative complementarity (%) are given only for the biggest samples. Sjk= Sj + Sk - Vjk, where Vjk = number of species shared by two microhabitats. C= complementarity.

Microhabitats	Orb weavers	Sheet-line weavers	Ambush predators	Cursorial hunters	Total	Species richness (Sjk)	C (%)
DRL-COM	28	35	22	57	142	347	59
DRL-VIN	19	22	17	25	83	249	67
DRL-DLV	-	1	4	5	10	-	-
DRL-EPI	10	20	3	29	62	229	73
DRL-PAL	3	17	7	-	27	-	-
DRL-MAU	4	-	-	-	4	-	-
DLV-COM	1	4	3	5	13	-	-
DLV-VIN	-	1	-	3	4	-	-
DLV-EPI	-	3	2	4	9	-	-
DLV-PAL	-	2	3	-	5	-	-
VIN-COM	18	28	21	40	107	306	65
VIN-EPI	8	19	5	17	49	182	73
VIN-PAL	2	15	6	-	23	209	89
VIN-MAU	2	-	-	-	2	-	-
EPI-COM	15	31	9	26	81	291	72
EPI-MAU	1	-	-	-	1	-	-
PAU-COM	2	8	2	8	20	282	93
PAU-DRL	4	-	1	6	11	210	95
PAU-VIN	2	3	2	4	11	-	-
PAU-EPI	1	5	1	3	10	-	-
PAU-PAL	1	5	1	3	10	-	-
PAU-MAU	1	-	-	6	7	-	-
PAU-PAE	2	4	2	3	11	56	80
PAE-COM	3	8	12	10	33	286	88
PAE-DRL	3	5	8	13	29	213	86
PAE-DLV	-	1	-	2	3	-	-
PAE-VIN	1	6	10	10	27	-	-
PAE-EPI	1	7	4	7	19	-	-
PAE-PAL	-	1	7	5	13	-	-
DRL-LUDD	14	18	7	4	43	353	88
DRL-LUDN	26	14	13	3	56	326	83
COM-LUDD	15	26	10	8	59	418	86
COM-LUDN	2	19	15	16	52	411	87

In general, the most common species found in the Samiria river have been also recorded from other Peruvian forests (Table 7), and most species shared by two or more microhabitats appear to be widespread in the Amazonian basin (Silva pers. obs.). However, the proportion of identified species is still low (less than 20 %).

DISCUSSION

In the Samiria river forest, most microhabitats were found to support a high diversity of spiders, despite any mismatching of males and females or unrecognized intraspecific variation.

TABLE 6

Degree of complementarity across canopy and understory microhabitats. Sjk = combined species richness; Vjk = number of species shared by two sets. COM=complex microhabitat, DLV= dry leaves & vines, DRL=dry leaves, EPI=epiphytes, MAU=*Mauritia* palm, PAE=*Scheelea* palm & epiphytes, PAL= *Scheelea* palms, VIN=vines.

Microhabitats	Species Richness	Vjk	Sjk	Complementarity (%)
DRL1 - COM1	137 vs 126	25	238	89
DRL1 - VIN1	137 vs 146	32	250	94
DRL1 - PAL1	137 vs 37	10	164	94
DRL1 - DRL2	137 vs 44	11	170	93
DRL1 - DRL3	137 vs 51	13	175	93
DRL1 - DRL4	137 vs 66	18	185	90
DRL1 - DLV1	137 vs 32	11	158	93
COM2 - DRL1	122 vs 137	28	231	88
COM2 (May-June)	122 vs 42	16	148	89
COM3 (May-June)	151 vs 87	27	211	87
COM3 - DRL1	151 vs 137	26	262	90
COM2 - COM3	122 vs 151	43	226	81
VIN1 - EPI1	146 vs 119	27	238	89
VIN2 - PAE1	55 vs 66	12	109	89
VIN2 - VIN3	55 vs 48	13	90	88
EPI1 - DRL1	119 vs 137	36	220	84
EPI1 - EPI2	119 vs 25	3	139	96
PAL2 - MAU1	39 vs 54	8	85	91
MAU1 - MAU2	54 vs 41	5	85	88

Although there were differences in sample size, canopy microhabitats showed, on average, a higher number of species and individuals than those in the understory. Nevertheless, the most complex microhabitats from the understory presented also a high species richness and density of spiders, sometimes as rich as those in the canopy.

It might appear that there is no strong division between canopy and understory in terms of species numbers and abundance when massive methods of collecting are employed. However, the species composition between these two strata is in fact drastically different.

It was rare to find dominant species in the fogging samples. Further, the most common spider species were distributed differently across various microhabitats. Typically, most species did not reach 0.5% of the total number of adult specimens for each fogging sample. Such results agree with other fogging studies from the understory and canopy of other tropical forests (HÖFER *et al.* 1994; RUSSEL-SMITH & STORK 1994; SILVA & CODDINGTON, in press). It has been shown that spider communities have few dominant species and that species richness and abundance vary not only according to forest type, altitude, or on a diurnal/nocturnal basis, but also with microhabitat qualities (i.e., fine differences in geomorphology, vegetation, microclimate, etc.).

Although the data at the present time show that most canopy microhabitats appear more distinct one from another than from any of the most heterogeneous

TABLE 7

Species richness and abundance of spiders from some Peruvian rainforests. Tambopata-Candamo National Reserve, some samples from fogging 1983-1984; Pakitza reserved zone, Manu National Park, conventional sampling, 1991; Samiria.

	SAMIRIA		PAKITZA		TAMBOPATA	
	Ind. (%)	Spp. (%)	Ind. (%)	Spp. (%)	Ind. (%)	Spp. (%)
ORB WEAVERS	1311 (22.2)	318 (27.9)	1242 (47.5)	235 (47.3)	225 (15.8)	108 (16.0)
Anapidae	26	3	2	1	2	2
Araneidae	853	207	743	145	91	75
Deinopidae	7	2	7	2	-	-
Mysmenidae	47	11	36	9	38	14
Symphytognathidae	6	2	-	-	-	-
Tetragnathidae	100	32	132	35	1	1
Theridiosomatidae	163	31	137	19	93	12
Uloboridae	109	30	185	24	-	4
SHEET-LINE WEAVERS	1702 (28.9)	233 (20.4)	876 (33.5)	111 (22.3)	554 (38.8)	146 (21.7)
Dictynidae	7	2	1	1	5	1
Hahniidae	1	1	-	-	1	1
Linyphiidae	38	10	25	6	43	14
Ochyroceratidae	1	1	-	-	-	-
Pholcidae	221	28	84	12	12	5
Rhoicininae	13	1	-	-	-	-
Scytodidae	78	6	19	2	15	3
Theridiidae	1343	184	747	90	478	122
AMBUSH PREDATORS	1114 (18.9)	180 (15.8)	237 (9.1)	67 (13.5)	119 (8.3)	172 (25.6)
Ctenidae	181	26	45	16	1	1
Hersiliidae	37	9	14	2	4	1
Heteropodidae	174	18	13	5	11	4
Mimetidae	103	23	59	11	13	4
Oxyopidae	39	17	29	8	14	6
Philodromidae	-	-	1	1	3	1
Pisauridae	140	28	27	3	2	1
Selenopidae	5	2	2	1	2	119
Senoculidae	19	2	18	4	6	4
Thomisidae	432	49	22	12	63	31
Trechaleidae	14	6	7	4	-	-
CURSORIAL HUNTERS	1768 (30.0)	409 (35.9)	261 (10)	84 (16.9)	529 (37)	247 (36.7)
Anyphaenidae	126	48	29	13	115	39
Aphantochilidae	36	2	5	1	1	1
Caponiidae	21	1	1	1	-	-
Clubionidae	10	3	3	3	36	-
Corinnidae	196	57	26	13	44	27
Gnaphosidae	67	12	1	1	6	4
Liocranidae	28	9	-	-	9	3
Lycosidae	106	12	22	6	-	-
Miturgidae	21	6	8	3	2	1
Oonopidae	402	31	6	3	73	34
Palpimanidae	1	1	-	-	-	-
Salticidae	747	220	160	40	243	129
Tetrablemmidae	1	1	-	-	-	-
Undetermined	6	6	-	-	-	9
TOTAL	5,895	1,140	2,616	497	1,427	673

understory microhabitats, it is necessary to take into account the effect of undersampling before making generalizations about degrees of faunal complementarity.

Undersampling is known to underestimate local species richness, ecological preferences, and geographical ranges, among other variables (COLWELL & CODDINGTON 1994). Such effects were obvious in the comparisons of single microhabitats and also when the spider fauna from the three Peruvian forests were compared (Table 7). It could appear that some taxa are absent or very poorly represented either in Tambopata or Pakitza; however, other data (Silva, pers. obs.) indicate that both localities are about as rich as the Samiria forest and, with exception of Tetrablemmidae, all other families are well represented in both sites.

While many spider species from the Samiria river appear to be recorded from other Amazonian forests, the taxonomic identity of most species is still uncertain and almost nothing is known about their true geographic distribution.

In general, the Neotropical spider fauna is still very poorly known. Many species collected in recent years are waiting for formal descriptions and many of the already known species present problems for accurate taxonomic identification. The latter were often described without the use of modern taxonomic criteria, were based on juvenile specimens lacking the structures necessary for accurate species identification, or were described from only one sex. All these factors contribute to an incomplete species inventory and, therefore, to a lack of accurate estimates of species diversity.

Finally, only further taxonomic work and phylogenetic analyses will provide the hypotheses needed to better assess distributional ranges and to clearly determine the historical factors responsible for the high species diversity found in the Samiria river. This information will make it possible to better establish the levels of distinctness among the microhabitats of the Samiria and other Peruvian rainforests, and, in turn, to provide a more rigorous scientific base from which to make conservation decisions regarding threatened areas in various tropical forests.

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Aspects of Spider Research in China

Daxiang SONG*
* Department of Biology, Hebei Teachers University,
Shijiazhuang, Hebei, 050016 China.

Aspects of spider research in China. - Research on spiders in China is closely associated with the need of agriculture. Since late 1970s, spider faunistic investigations in mountainous areas as well as on farmland have been undertaken in collaboration with plant protectors in many provinces. For assessing the role of spiders in the control of insect pests, studies of dominant species were carried out on their growth and development, longevity, courtship and mating, oviposition and progeny potential, feeding habit and predation on insect pests including functional response of them to prey population densities. In order to get more data for comparison, as usual, the spiders were reared and observed indoors as well as outdoors. In addition, the toxicity of pesticides to different dominant species of spiders have been tested. Up to date, Chinese arachnologists have published hundreds of papers on spider taxonomy and biology. Also, fourteen books dealing with spiders of China or provincial faunas have been published. Besides, three volumes of *Fauna Sinica* on spiders (Araneidae, Theridiidae, Thomisidae and Philodromidae, respectively) are being compiled.
China has a vast territory with a complex climate and topography. It is roughly estimated that there are at least 3,500 species of spiders in China warranting careful investigation.

Key-words: China - spiders - agriculture - fauna.

The first National Conference of Arachnology of China was held in Kunming, the capital of Yunnan, in June 1983 and the China Arachnological Society, as one of the 13 subsocieties of the China Zoological Society, was established in July 1986, marking the milestone in development of Arachnoloy in China. In the rnid-seventies, Chinese agriculture workers found that spiders were so abundant on the farmland that they presumably should play an important role in control of insect pests. Afterwards studies on spiders began to be carried out in many agricultural institutions. The utilization of spiders in biological control has brought about a great advance in researches on spiders not only in the aspects of biology but also in taxonomy. So the

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uprising of the research work on spiders in the past two decades is closely associated with the need in agriculture. Since then, "combat bugs with bugs" or "combat bugs with spiders" — this biological philosophy for the control of crop pests have been beginning to win widespread popularity among farmers, with the added bonus of cutting crop protection costs and insecticide pollution.

Comparing with insect parasites and other predators, spiders as a natural enemy of insect pests have the following advantages.

1. Spiders are abundant in the field. In general, the spider populations account for 60-80% of the total number of predators. Thus it means spiders are the most important component of predators.

2. Spiders are indiscriminate and voracious feeders. Spiders rarely reject any prey and they may suppress a wide range of pests. A tiny dwarf spider consumes about 2 planthoppers (*Nilaparvata lugens* Stål), daily. One median-sized spider consumes about 6 insects daily.

3. Spider usually appears in the field earlier than insect predators. For example, crab spider *Philodromus cespitum* (Walckenaer) in North China is found on the cotton seedling at least one month earlier than predacious insects. They capture cotton aphids at an earler stage to prevent the outbreak of aphids.

4. Under the circumstances of lacking food spider can survive for a long time. *Hylyphantes graminicola* (Sundevall) can live without food for 15–31 days and *Pardosa pseudoannulata* (Boesenberg & Strand), 56–116 days. When there are no insects for a certain period of time, spiders will not die with hunger. When the insect pests begin to reproduce, spiders would be activated for capturing them.

5. Spiders live in the same environment with the insect pests and they have high fecundity. *H. graminicola* produces 6–7 generations a year. Each generation produces about 10–15 egg sacs, each containing 40 eggs or so. *P. pseudoannulata* reproduces 2–3 generations a year. Each generation produces 4–7 egg sacs with about 120 eggs in each cocoon, sometimes even 200 eggs. They can live and multiply in the field for a long time. As for dwarf spiders, they can live 6–12 months, and the median-sized wolf spiders can live 1–2 years.

With the characteristics mentioned above spiders can be well used in biological control in addition to other natural enemies. Rearing and releasing are rather costly and failure may be due to bad weather. Most agriculture workers divert their attention to the protection of spiders.

Then what are the threats to affect the survival of spiders? One is farming activities, including ploughing, flooding, and crop harvesting, the other is insecticide application. Both can reduce the population of spiders in the field by 30–99%, the result could be the outbreak of pests afterwards due to the fact that the rates of growth and reproduction of spiders are lower than those of the pests

Different measures are adopted to preserve spiders in accordance with different culturing practices, such as: 1. Putting bunches of rice straw before ploughing or flooding and then taking them away to a field where spiders are needed. As usual, each such bunch may contain 400–700 spiders, some up to 1000 spiders. 2.

Inter-planting or arranging a "bridge-field" for spider transferring from one field to another one. 3. Leaving the border field not weeded to provide a place for the hiding of spiders. 4. Digging some holes near the farmland and covering them with straw as a shelter for spiders. Investigation showed that at first the number of pests might be equal to or higher than that of predators, but as time goes on the pests become fewer and fewer because of being eaten by their natural enemies. This is especially important for spiders living through the summer or winter. In addition, to tie bunches of straw on tree trunks is also useful for spider preservation.

Regarding the effect of application of insecticides, studies were carried out first to assess the role of spiders in the control of insect pests. Studies of every dominant species were carried out on their growth and development, longevity, courtship and mating, oviposition and potential of progeny multiplication, food habit and predation on insect pests including functional response of them to prey population densities. In order to get more data for comparison, as usual, the spiders were reared and examined under laboratory condition as well as at outdoor condition.

Agriculture workers have to estimate the ratio of spiders to the pests first. For example, in area of double cropping of rice in South China, if their population ratio (spider: hopper) in the early crop is 1:3–4, or 1:5–9 in the later crop (this depends on the dominant species of spiders present at the time), no outbreak of leafhopper (*Nephotettix cincticeps* (Uhler) and planthopper will occur. The agriculture technicians of the County Bureau of Agriculture or of Corporation have to collect and analyse the data from the plant protectors at the basic level, and then make the decision of using or not using insecticide, and if use, teach the method and amount of insecticide applied. If insecticide is necessary, its applications are usually confined to a part of acreage, to individual fields, or even to infested spots within a field.

This decision depends on the ratio of the natural enemies (especially spiders) to the pests, the growth and development of crop, etc. Emphasis is laid on whether in the key period of the coming 2–3 days spiders can depress the main pests below the threshold density. This is to say, although the ratio now is a bit higher, yet it will reduce to a point which we define or expect in several days later (it depends on the nutrition of crop), insecticide may be not used.

Selection of the correct insecticide and formulation are important not only for effective pest control but also for conservation of natural enemies. The toxicity of pesticides, to different dominant species of spiders has been tested by Chinese arachnologists. These studies are carried out not only on the different kinds of pesticides, but also on different formulations and methods of application. In a word, every effort has been made to minimize the adverse effects on spiders.

Along with the study on use of spiders as natural enemies to control insect pests the study on the taxonomy of spiders has also been developing. Beside our expedition to different provinces for collecting spiders, every year lots of specimens are sent from all regions of the country by agriculture workers for taxonomic identification. To meet the need from basic unit of the country at first we examined and identified the specimens collected from rice, wheat and cotton crops as well as from

fruit trees. So we started our work on the spiders which occur frequently in farmland or groves and are of more economic irnportance, such as families of Araneidae, Clubionidae, Lycosidae, Thomisidae, Tetragnathidae, Linyphiidae and Salticidae.

Although spiders were observed and reported in ancient China, arachnology as a branch of modern biology was introduced from the west in the nineteenth century. Early works dealing with Chinese spiders by foreign arachnologists can be listed as follows: Donoran (1798), Cantor (1842), Pryer (1868), Butler (1873), Koch, L. (1875), Simon (1880, 1885, 1886, 1888, 1895, 1901), Karsch (1881), Cambridge (1871, 1885), Lendl (1897), Pocock (1901), Strand (1907, 1909, 1910), Hogg (1912), Berland (1914), Chamberlin (1924), Gerhardt (1927), etc. Of them, Simon's paper (1880) on spiders from Beijing and its vicinity is most important. Some species (such as *Xysticus ephippiatus* Simon) described by him in the paper are very common in the fields.

The first Chinese zoologist who reported spiders was Prof. PING, C. In his papers dealing with the faunas of Nanking (1931) and of lower Iangtze in 1932, he noted about 33 genera of spiders in the city of Nanking and its suburbs. Though not an arachnologist he identified and listed some specific names of spiders correctly then, such as *Agelena labyrinthica* (Clerck), *Lycosa pseudoannulata*, *Scytodes thoracica* (Latreille), *Uroctea compactilis* L. Koch, *Oxyopes sertatus* L. Koch, and *Nephila clavata* L. Koch, etc. The first reports on spiders by Chinese arachnologists were not appeared until the year of 1963. Prof. WANG, F.Z. & ZHU, C.D. published 4 papers on spiders in the J. of Jilin Medical University.

Due to the need of agriculture as mentioned above, some zoologists turned their research topics to Araneae. In 1976, Song, D.X., Huang, Q.L., Feng, Z.Q. & Wang, H.Q., first noted some tetragnathids from the rice field of Zhejiang Province. After that, a new period in arachnology of China started. Up to date, Chinese arachnologists put out hundreds of papers on taxonomy, biology and spermatogenesis in spiders. Some of them were coauthored with American, German, Japanese and Korean colleagues. Also, fourteen books of spiders or provincial faunas have been published, namely: "Farmland Spiders" (Writing Group of "Farmland Spiders", 1980), "Protection and Utilizaton of Spiders in the Rice Fields" (WANG, H.Q., 1981), "The Spiders from Agricultural Regions of China" (SONG, D.X., 1987), "The Chinese Spiders Collected from the Fields and the Forests" (HU, J.L., 1984), "Spiders in the Cotton Fields in China" (ZHAO, J.Z., 1993), "Spiders in China, One Hundred New and Newly Records Species of the Families Araneidae and Agelenidae (Arachnida: Araneae)" (YIN, C.M., WANG, J.F., XIE, L.P. & PENG, X.J., 1990), "Salticids in China (Arachnida: Araneae)" (PENG, X.J., XIE, L.P. & PENG, X.J., 1993); "Spiders from Agricultural Regions of Xinjiang Ugygur Autonomous Region, China" (HU, J.L. & WU, W.G., 1989), "The Sichuan Farmland Spiders in China" (CHEN, X.E. & GAO, J.C., 1990), "Spiders from Farmland of Shaanxi, China" (GUO, J.F., 1985), "Araneae, Fauna of Zhejiang Province" (CHEN, Z.F. & ZHANG, Z.H., 1991), "Spiders from Farmland of Shanxi, China" (ZHU, M.S. & SHI, J.G., 1983); "Spiders from Farmland of Hebei, China" (ZHANG, W.S., 1987), "The Spiders Collected from the Fields and

Forests of Xizang Autonomous Region, China" (Hu, J.L. & Li, A.H., 1987). Besides, three volumes of *Fauna Sinica* on spiders (Araneidae, Theridiidae, Thomisidae and Philodromidae, respectively) are being compiled.

At present, most researches have been carried out by the following units: Hubei University in Wuhan, Hubei Province (biology), Institute of Zoology in Beijing (systematics), Hunan Normal University in Changsha, Hunan Province (systematics and biology), Hebei Teachers University in Shijiazhuanmg, Hebei Province (systematics), and Dr Norman Bethune University of Medical Science (former Jilin Medical University) in Changchun, Jilin Province (systematics). China Arachnological Society is now attached to the Hubei University. Plenary meeting is organized biennially by the society and a publication of *Acta Arachnologica Sinica* is issued from 1992, semiannually.

China is a vast country with complex topogeography and climate. It crosses frigid, temperate and tropical zones from north to south. Plateaux and high mountains occupy over 50 percent of land. Biogeophically, China is situated in both the Palaearctic and Oriental Realms. During the late Tertiary period, most regions had not been effected by glaciation, thus the fauna and flora is characterized by having many endemic and relic species. Therefore, it is considered internationally that China is one of the megadiversity countries in the world, where the number of species makes up about one tenth of the total number of species of the world. It is hard to say exactly how many species of spiders there are in China. But it may be roughly estimated that there are at least 3,500 species. Considering most species threatened by deforestation, habitat change, indiscriminate use of pesticides and other human impacts, it is urgent to organize large-scale surveys on China's fauna of Araneae, especially in provinces like Yunnan and Hainan. In order to keep the work on spiders flourishing, more funds, manpower and international collaboration are needed.

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Courtship behaviour in the spider *Pityohyphantes phrygianus* (Linyphiidae, Araneae): do females discriminate injured males?

Pia STÅLHANDSKE* & Bengt GUNNARSSON
Section of Animal Ecology, Department of Zoology, Göteborg University, Medicinaregatan 18, S-413 90 Göteborg, Sweden.

Courtship behaviour in the spider *Pityohyphantes phrygianus* (Linyphiidae, Araneae): do females discriminate injured males? - Courtship behaviour was studied in the sheetweb spider *Pityohyphantes phrygianus* (C.L.Koch). The courtship, involving virgin females and previously unmated males, consists of three major phases with regard to male behaviour: (1) shaking of abdomen when touching the female's web; (2) reduction of the web area; and (3) pseudocopulation. The female is mainly inactive during courtship but raises her abdomen from a horizontal position before the male terminates web reduction.
In wild populations, males with leg injuries are common; approximately 16% of the males in the study population showed such injuries. Therefore, in experimental males, one of the forelegs was shortened 44% before courtship. Males with asymmetric legs performed the initial phase of pseudocopulation less well than normal males. Injured males had difficulties in finding a suitable position and the number of short breaks at the beginning of pseudocopulation were more frequent than in normal males. Consequently, experimental pairs spent a longer time finding a stable mating position. However, no female discrimination of males with an amputated leg was observed. It may be potentially dangerous for females to reject a male since the sex ratio, both primary and secondary, is highly female biased in natural populations.

Key-words: Female choice - courtship behaviour - injured males - asymmetry - spider - web reduction.

INTRODUCTION

The function of spider courtship has been debated ever since late 19th century (Robinson 1982). One hypothesis is that the courtship provides the female with information about male quality, i.e. intersexual selection (Robinson 1982, Watson 1990).

*Correspondence to P. Stålhandske.
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Leg injuries among males are common in natural spider populations (unpubl. obs.). Such injuries may arise in several ways. Many specimens save themselves from a predator's attack by separating a leg from the rest of the body (FORMANOWICZ 1990). Furthermore, fighting between males may result in loss of forelegs (DODSON & BECK 1993). If a leg is broken at a joint, the hemolymph pressure forces the joint membrane to seal the wound (FOELIX 1982). Shortened legs in the adult stage may also be caused by incomplete, or partly unsuccessful moulting (Gunnarsson unpubl.). Thus, it is possible that females may use injured legs as a cue for assessing male quality. Alternatively, the females do not discriminate damaged males because other aspects of their mate are more important.

If injured males perform a courtship that is different from the behaviour of normal specimens, females may reject such males. A rejection is plausible if the behaviour signals inferior quality or if the female experiences higher risks, e.g. due to predation during courtship. However, another alternative is that females do not discriminate between injured and normal males. This would be expected if the altered male courtship behaviour does not affect female fitness in any way, or if the females are unable to detect the injury, or if females for some reason mate with the first available male. The latter expectation would e.g. be probable if the operational sex ratio is female biased.

In the present study, we examined the courtship behaviour in normal and injured males of the sheet web spider, *Pityohyphantes phrygianus* (C.L. Koch, 1870) and the females' response to courtship. Injured males were produced by shortening one foreleg by approximately 44%. We define courtship as the male behaviour from detecting the female's web until the onset of sperm transfer. Given that visual signals are of little importance in many spider families, including linyphiids, the web seems to provide the male with some information about the reproductive status of the female (unpubl. obs.). The copulation in linyphiids is preceded by a pseudocopulation, where normal copulation behaviour is performed but no sperm is transferred (VAN HELSDINGEN 1965, AUSTAD 1982, SUTER 1990). We included this behaviour in our study of the courtship in *P. phrygianus*.

METHODS

Subadult spiders were collected at two coniferous forest sites in SW Sweden about 20 and 30 km east of Göteborg. The collecting was done between late March and mid April 1993. We enclosed the needle-carrying parts of spruce branches in a plastic sack and shook the branches vigorously. The spiders were sorted out from the debris and were kept separately in plastic vials closed with a cotton ball.

In the laboratory the specimens were initially kept at 4°C. After 10-44 days they were brought to room temperature (20°C). Before moulting the males were randomly placed in three groups: (1) untreated males (N=19), (2) males that were anaesthetized with carbondioxide (N=8), and (3) males that were anaesthetized and had one foreleg surgically amputated with a scalpel just below the patella (N=20), i.e. tibia, metatarsus and tarsus were removed. All treatments were made within two days.

Whether the left or right leg was amputated was decided at random. The amputated legs were not regenerated after the final moulting. Five specimens in group (3) were adults when the leg was amputated. All specimens survived the amputation treatment and no decreased vigour was observed.

The time until moulting in room temperature was 3-10 days for females and 1-3 days for males (cf. GUNNARSSON & JOHNSSON 1990). After treatment and moulting the specimens were kept in 10°C until the experiment started. The courtship experiments were conducted on May 10-19 and 29, 1993. The females were brought to room temperature 72 h before the experiment started and each of them was placed in a 500 ml plastic vial equipped with spruce twigs. In each trial (N=47), one previously unmated male was introduced into the web of a virgin female. Each individual was used only once. When introduced, males were carefully placed in the web and as far away from the female as possible. The courtship was considered to have started when the male shook his abdomen for the first time. Shaking consisted of a rapid vertical jerking of the abdomen and this time was set as t=0. The spiders were observed until a pseudocopulation had lasted for 50 minutes without interruptions, or until three hours had elapsed. Special attention was given to the female's behaviour, i.e. the time the female raised her abdomen, and the start of pseudocopulation. After 24 h we separated the pairs and the specimens were weighed. Female weight was 7.54 ± 1.25 mg (N=43) and male weight was 7.56 ± 1.37 mg (N=42). There were no weight differences between groups (1)-(3), either among females or males (Kruskal-Wallis ANOVA, P=0.80, N=43 and P=0.59, N=42, respectively).

No food was provided before or during the experiment, but water was available in the vials. After termination of courtship experiments, 10 females from group (1), 4 females from group (2), and 11 females from group (3) were randomly choosen. These specimens were fed, and we recorded oviposition and hatching success.

We used non-parametric statistics in the analyses because we suspected non-normal distribution of the data. All means are given together with their S.D., unless otherwise stated. Sample size in the text refers to total number of specimens in each group.

RESULTS

Courtship of normal males

All males except of one carried out courtship behaviour. When introduced into the female's web, the male's courtship started almost immediately. Within two minutes 89% of the males began to shake their abdomen; the mean time was 3.3 ± 9.5 min. (N=18). The shaking was of short duration and was followed by a period of quiescence (Fig. 1). The female remained inactive during this first phase.

The second phase of courtship consisted of a reduction of the web area (Fig. 1). Biting off all but a few of the supporting silk threads, the male reduced the sheet web to a small wad. During the web reduction phase, the male approached the female

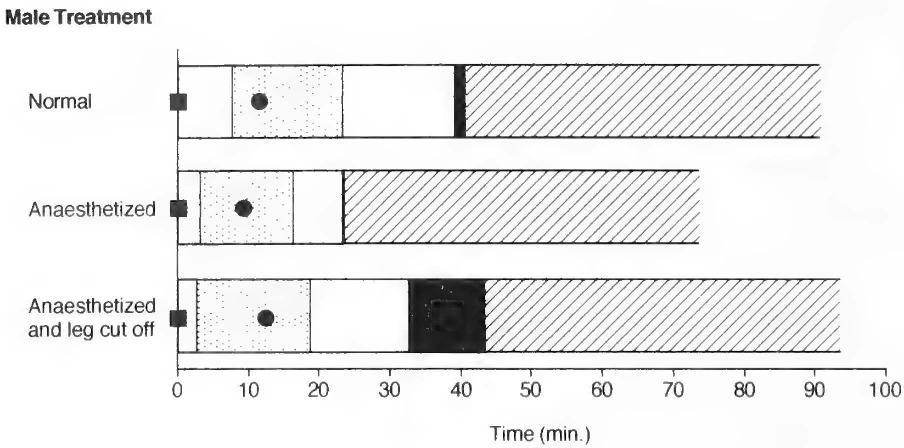

FIG. 1

Timing of courtship activities. First phase: male shaking his abdomen (■). Second phase: web reduction (▭) and female raising her abdomen (●). Third phase: pseudocupulation, with short breaks (▬), and continued for at least 50 min. (▨). Phases were separated by periods of no activity (▭). The beginning and ending of each phase are defined by mean values (min.). Pseudocupulation continues beyond what is shown.

TABLE 1

Female behaviour during second phase of the courtship (A and B), and time elapsed until initiation of pseudocopulation (C) (cf. Fig. 1). P denotes the significance level between treatments in a Kruskal-Wallis one-way ANOVA.

Male treatment	A. Female raising her abdomen (min.)			B. Number of interruptions in the female's mating position			C. Pseudo-copulation initiated (min.)		
	Mean	(S.D.)	N	Mean	(S.D.)	N	Mean	(S.D.)	N
Normal	11.2	(8.0)	18	1.6	(1.8)	11	39.0	(29.6)	18
Anaesthetized	9.2	(7.7)	8	2.4	(1.3)	8	23.3	(7.3)	8
Anaesthetized and leg amputated	12.4	(8.5)	20	1.9	(1.4)	20	32.6	(20.4)	20
P	0.52			0.52			0.38		

and lightly touched her legs. Almost half of the males (44%, N=18) started to bite off silk threads before they had touched the female. However, these males intensified web reduction activity after having touched the female. During the male's web reduction, the female raised her abdomen from a horizontal to a more or less perpendicular position (Tab. 1) (Fig. 1), producing an angle of approximately 60° between the ventral part of the abdomen and the horizontal plane. The female sometimes left this position (Tab. 1), e.g. after violent web reduction activity by the male. A quiet period followed the web reduction phase (Fig. 1). The male resided in the vicinity of the female and the pair often touched each other's forelegs.

During the third courtship phase, the pseudocopulation, normal copulation behaviour was performed but no sperm was transferred. The female, still with raised abdomen, waited in the reduced web. The male, waving his legs, approached the female whereupon the pair immediately assumed the mating position and pseudocopulation was initiated (Tab. 1) (Fig. 1). In some pairs, short breaks occurred at the beginning of the pseudocopulation phase. The pseudocopulation was initiated, on average, 1.8 ± 1.2 times (N=18) and the pair spent 1.6 ± 5.0 min. to find a stable mating position. However, more than half of the pairs (56%) succeeded in carrying out pseudocopulation the first time they entered the mating position (Fig. 2).

No female attacked or cannibalized her male partner during courtship or the rest of the cohabitation. All females that were fed after a period of 24 h together with the male oviposited and produced spiderlings.

Courtship by experimental males

All males that were treated by anaesthetization (N=8) and/or foreleg amputation (N=20) carried out the courtship. During the first and second phase of the courtship, we analysed the response of the female towards the male. We found no significant differences in the female's behaviour among the three groups of males, i.e. the time for the female's first mating position, number of interruptions, and the start of pseudocopulation (Tab. 1). During the third phase, however, short breaks at the beginning of the pseudocopulation were more common among males with an amputated foreleg. Only 25% (N=20) of these males managed to bring the pseudocopulation to an end in the first entered mating position (Fig. 2). When entering the mating position, they slipped down to the side and had difficulties to reach the female's epigyne. There were differences among the three groups in the number of mating positions initiated (P=0.056, Kurskal-Wallis one-way ANOVA, N=46) (Fig. 2). The groups with normal and anaesthetized males were similar (Multiple comparisons) (see Fig. 2), indicating that anaesthetization did not affect courtship behaviour. Therefore, they were pooled in further analyses. Males with amputated legs made more attempts (mean 4.4 ± 6.1, N=20) before finding a stable mating position than pooled males (mean 1.8 ±1.2) (P=0.018, Mann-Whitney U-test, N_1=20, N_2.=26). Consequently, pairs in which the male had a shortened leg spent a significantly longer time (mean 10.9 ± 22.7 min. N=20) finding a stable mating position than pooled pairs (mean 1.2 ± 4.2 min. N=26) (*P*=0.022, Mann-Whitney U-test, N_1=20, N_2=26) (see also Fig. 1).

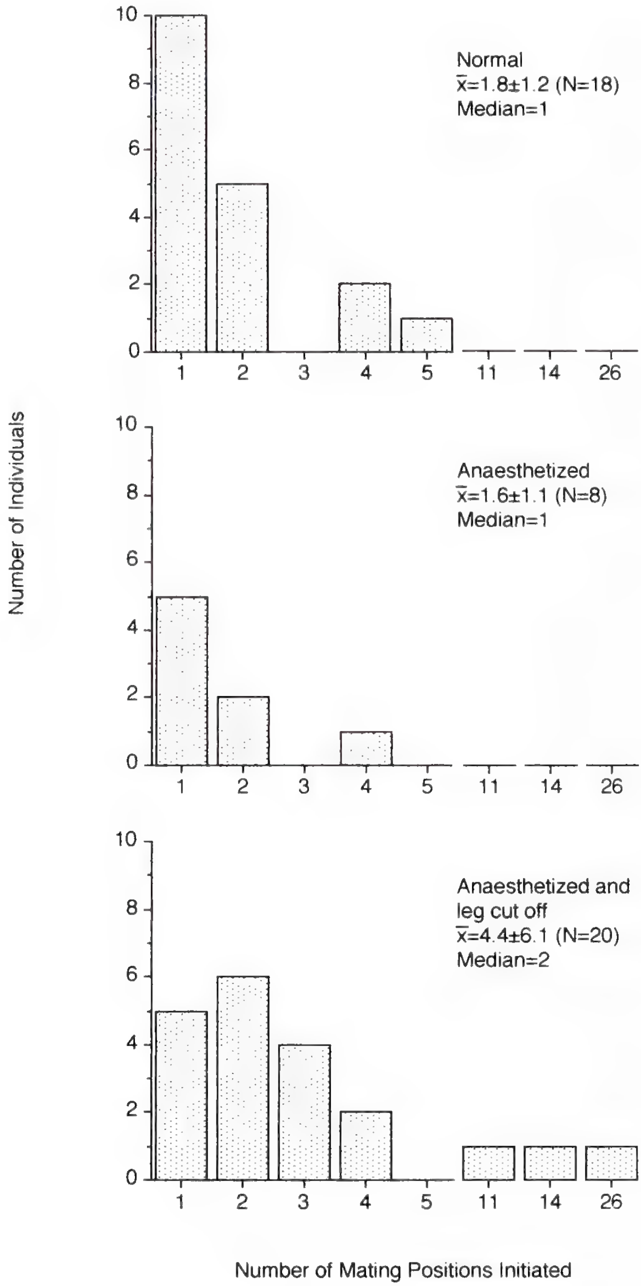

FIG. 2

Male behaviour at the beginning of pseudocopulation. The number of mating positions initiated by males in treatment groups.

Males that had their right leg amputated (N=8) had more difficulties when entering the mating position than males with the left leg amputated (N=12). Males with a shortened right leg made more attempts (8.0 ± 8.6) before a pseudocopulation was completed than did males with a shortened left leg (2.0 ± 1.0) (P=0.027, Mann-Whitney U-test, N_1=8, N_2=12); They also spent more time (22.1 ± 31.6 min.) finding a stable mating position than did males with the left leg amputated (3.5 ± 10.3 min.) (P=0.018, Mann-Whitney U-test, N_1=8, N_2=12). Unfortunately, by chance the female's mean weight was lower within the group of males that had their right leg amputated (6.9 ± 0.9 mg) compared with the group of males that had their left leg amputated (8.2 ± 1.6 mg) (P=0.042, Mann-Whitney U-test, N_1=7, N_2=11). There were, however, no significant correlations between female weight and number of matings initiated, or time to find a stable mating position (P>0.5 and P>0.2, respectively, Spearman rank correlation test, N=42).

No female attacked her male partner during courtship. One anaesthetized male and two males with an amputated foreleg were eaten by the female within 24 h. All experimental females that were allowed to oviposit produced spiderlings, i.e. males were cannibalized after they had transferred sperm.

DISCUSSION

In *P. phrygianus*, females obviously allow injured males to mate although their courtship behaviour during pseudocopulation is different from that performed by normal males. Males with an amputated leg often seemed to have difficulties in finding appropriate position during the early phase of pseudocopulation. The female should have ample possibilities to reject an inferior male during courtship, and feeding on a male may even increase her future fitness. The female raised her abdomen before the male had finished the web reduction. It is not known what this behaviour means to the male. The female probably allows the male to start pseudocopulation but she has still the possibility to reject the male since no sperm has been transferred so far. Courtship among arthropods is usually performed in sequence and often the female has the option of rejecting the courting male at any stage (e.g. STEEL 1986*a*, *b*, ELGAR & NASH 1988). However, courtship may serve several functions and males and females often have conflicting interests even before the mating is initiated.

There may be several reasons why females do not reject injured males. First, there is a possibility that females rarely contact "damaged" males in nature and that they are unable to detect the injury. Second, there may not be any fitness gain in being discriminating. A third alternative is that the cost of rejection is too high.

How common are injured males in natural populations? If it is rare that males with injuries perform any courtship, then a discrimination by the females might be irrelevant. Out of 185 males collected for the present and other experiments, thirty specimens (16.2%) had one or more legs that were shortened or injured in some way. This suggests that males with leg injuries are common in the wild and that females may encounter such males quite often.

In the present study, we used males with strongly asymmetric forelegs. The forelegs are used in the communication between the sexes during courtship, i.e. the male touches the female lightly with the forelegs. The results indicated that asymmetric males performed "bad" courtship, acting clumsily during pseudocopulation. There are reasons to believe that females are able to detect the different behaviour of injured males in comparison with normal males. A study on *Linyphia litigosa* showed that males with injured or missing legs were avoided by remating females (WATSON 1993).

One reason to expect that females should reject males with an amputated leg is increased predation risks due to prolonged courtship. There were more attempts to start pseudocopulation in injured males than in normal ones. Consequently, injured males moved around in the web more frequently and the time until finding a stable mating positon was longer than for males without leg injuries. Thus, on average, an injured male performs a longer courtship which increases the exposure of himself and the female to visual predators. The pseudocopulation continues for a much longer time but then the male and female remain in mating position without moving around. The females may therefore be selected to reduce the courtship time. This was supported by the fact that females were willing to initiate the pseudocopulation (i.e. raising abdomen) before the males had finished web reduction. Presumably, the purpose of reducing the web area is to reduce the probability that male rivals will detect the female (data on other linyphiids, cf. ROVNER 1968, WATSON 1986), and consequently the courting male performs his task carefully.

The reason why females did not discriminate injured males is probably that the sex ratio is female biased in this species. *P. phrygianus* has a skewed primary sex ratio, averaging one-third of males and two-thirds of females (GUNNARSSON & ANDERSSON 1992). Furthermore, in severe winters, male survival declines considerably which may result in a sex ratio of 1 male: 9 females, or less (GUUNNARSSON 1987). This means that there is great annual variation in operational sex ratio, i.e. the ratio of sexually active females to males (EMLEN & ORING 1977) during the reproductive period in spring. Moreover, there are fluctuations in the operational sex ratio within the season as males mature before the females (GUNNARSSON & JOHNSSON 1990). A virgin female that is choosy may take a substantial risk to remain unmated. Under such a condition females should be selected to mate with the first male available.

It is unclear why males with their right foreleg shortened had more difficulties entering the mating position than had males with their left leg amputated. It suggests that one type of asymmetry is worse than the other. This may be a consequence of fine adjustment during the pseudocopulation due to signals between the sexes. Both palps are used during the pseudocopulation but it is unknown whether there are special sequences of left and right insertions. This warrants further investigation.

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Observations on the mating systems of two spiders, *Linyphia hortensis* Sund. and *L. triangularis* (Cl.) (Linyphiidae: Araneae)

Helmut STUMPF & K.E. LINSENMAIR
Theodor-Boveri-Institut für Biowissenschaften, Zoologie III, Biozentrum, Am Hubland, Universität Würzburg, D-97074 Würzburg, Germany.

Observations on the mating systems of two spiders, *Linyphia hortensis* **Sund. and** *L. triangularis* **(Cl.) (Linyphiidae: Araneae). -** Observations on the phenology of the spiders, the operational sex ratio, precopulatory mate guarding and fighting behaviour are reported. Differences in the copulatory behaviour like remating probability of females and sperm priority patterns are discussed.

In both species males mature before the females and the operational sex ratios are male biased. Males guard subadult females until their final moult and defend them against intruders. Male fights in *L. triangularis* are longer, more intense and riskier than in *L. hortensis*. In *L. triangularis* receptive females are present only for a short period because most subadult females moult within a few days, copulating males seal the copulatory openings of the females with mating plugs and remating probability of females in the laboratory is very low. In *L. hortensis* receptive females are to be found during a prolonged period since they are less well synchronized in their final moult, they may copulate more than once and second males can fertilize a small portion of the females eggs. Therefore copulations with virgin females are probably more valuable to *L. triangularis* males than to *L. hortensis* males. Because males should adjust their investment of energy and time into fights according to the expected gains the differences in the mating patterns and the availability of receptive females are probably responsible for the observed differences in the fighting behaviour of the males of the two species.

Key-words: mating systems - Linyphiidae - phenology - mate guarding - fighting behaviour - remating probability

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INTRODUCTION

The mating system (or mating pattern) of a species can be defined as the relationships and interactions between females and males in the context of reproductive behaviour. It comprises a specific set of behavioural mechanisms and adaptations which have evolved under the influence of the often conflicting reproductive interests of the two sexes and species-specific or population-specific ecological constraints.

In this paper a short summary will be given of the mating systems of two closely related species of linyphiid spiders, *Linyphia hortensis* and *L. triangularis*. We focus here only on a few important factors which shape and characterize the mating systems with our main interest directed to the intensity of intrasexual competition in males. The factors considered here are as follows: (1) the temporal availability of mates, (2) the behavioural mechanisms males use to optimize their reproductive success and (3) the females' remating behaviour.

Therefore we will present data on the phenology of the two *Linyphia*-species (length and timing of male and female moulting periods), the operational sex ratio (i.e. the ratio of receptive females to sexually active males at any given time, Emlen & Oring 1977), the guarding and fighting behaviour of the males and the remating probability of the females. Common features of the two mating systems and differences between them will be outlined and possible behavioural consequences will be discussed.

Natural history of the species

Both *Linyphia* species are very common and widespread in Europe, *L. hortensis* prefers shady habitats like woods and hedges, whereas *L. triangularis* lives in almost any location where a shrub layer is present. Webs of both species are mostly located in the upper part of the herb layer, *L. triangularis* webs can also be found in the lower parts of the shrub layer. The webs are typical sheet webs with a horizontally oriented web sheet and irregular mesh-works of threads above and below this sheet. The species have an annual life cycle with a rather short reproductive period: *L. hortensis* reproduces in spring and early summer (April to June), whereas the reproductive period of *L. triangularis* is in summer and fall (July–September).

METHODS

Investigations were carried out between 1987 and 1993. Data from several years were pooled if there were no significant differences between years. Field observations were made in appropriate habitats near Würzburg, Southern Germany (*L. hortensis*: in a deciduous forest with a well developed herb layer, *L. triangularis*: in a garden with hedges).

The phenology of the two species was investigated by surveying 100–200 webs per day throughout the reproductive period. For the analysis months were divided in three parts of 10–11 days (decades).

Observations on the guarding behaviour of males were made at marked webs of subadult females which were checked at least twice a day. The time from the day of the first appearance of a male in a web to the day of the female's moult was taken as the measure for guarding duration if, on all subsequent controls, a male was present in the web. Since only few guarding males were marked individually and web-take overs were frequent this method gives no appropriate measure for the guarding duration of individual males.

Male visitation rates in webs of subadult and adult females were obtained by continuous observations (0,5–8 hours) at webs in the field (*L. hortensis*: 265 hours at 48 webs, *L. triangularis*: 387 hours at 134 webs). Male visits < 0,5 min were ignored.

In the laboratory male fights were staged in the webs of virgin females that were removed before the males were simultaneously put into these webs. The weight difference between the contestants was measured as % of the smaller male's weight.

The sperm precedence pattern was investigated in *L. hortensis* by assessing the reproductive success of sterile males in sequential copulations. Males were sterilized by X–ray or γ–radiation. A dosis of 5 Krad led to complete sterility in the males (n = 59 control copulations) without affecting the copulation behaviour. Sterile males were used only once a day. The reproductive success of second males was assessed by comparing the fertilization rates in the first three cocoons of females which had copulated successively with a sterile and a fertile male with that of females that had copulated with fertile males only.

The remating probability of females was assessed in the laboratory by testing the disposition of females to mate again with a second male after a completed first copulation. The test duration was 1–2 hours. Female behaviour during that period proved to be a reliable predictor for the subsequent behaviour.

RESULTS

Temporal availability of mating partners

The percentage of juvenile females and males during the course of the reproductive periods of both species is shown in figure 1 (data of several years pooled). In both species almost all subadult males moult considerable earlier than females. In *L. hortensis* most males mature at least 3 to 4 weeks before the females. In favourable years some males may even moult in the previous autumn and hibernate as adults. First adult males of *L. triangularis* can be found about 2 to 3 weeks earlier than adult females. In both species almost all males are adult and sexual active when the first females begin to moult.

One important difference between the two species is the length of the moulting period of the females: in *L. hortensis* moulting females can be found over a period of 6 to 7 weeks, while in *L. triangularis* almost all females moult within 3 to 4 weeks.

Male guarding behaviour

The percentage of female webs in which males are present is shown in figure 2. In both species almost all females were guarded by males at the day of their final

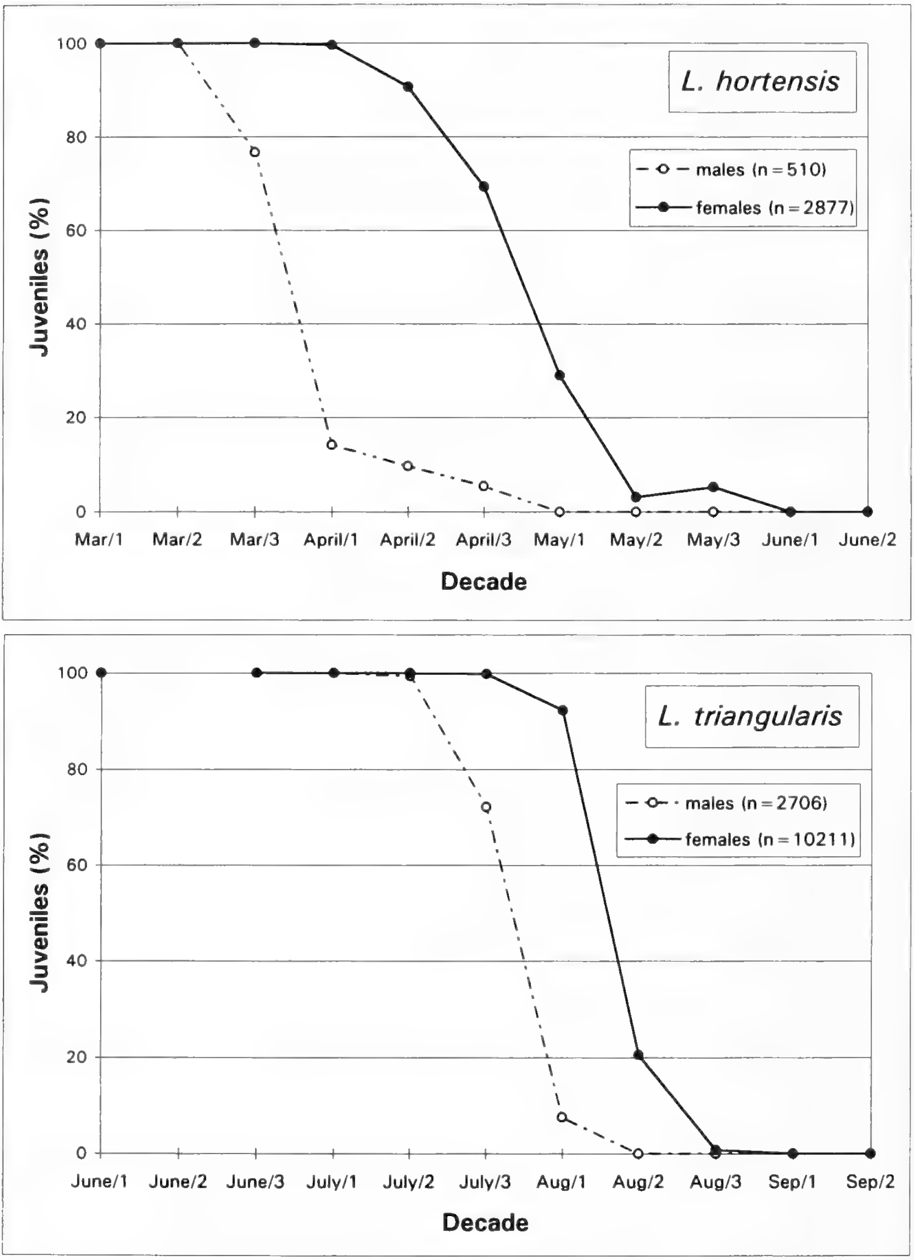

FIG. 1

Phenology of *L. hortensis* and *L. triangularis* near Würzburg, Germany: Percentage of juveniles and subadults, separated by sex (data from several years pooled, each month divided in three decades).

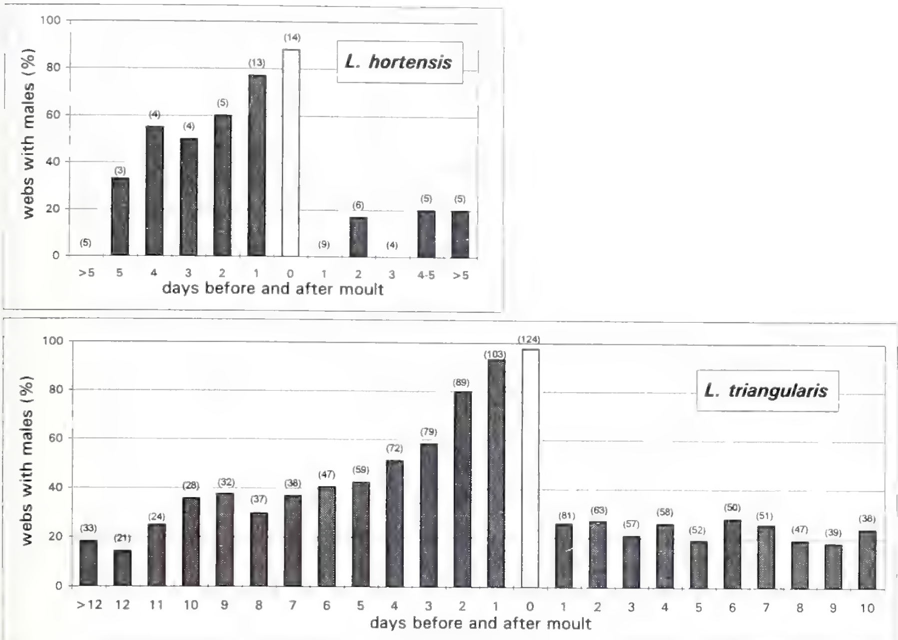

FIG. 2

Web guarding in *L. hortensis* and *L. triangularis*: Percentage of female webs with males present before and after the females' moult (day of moult = 0, sample sizes in brackets = all webs)

moult (*L. hortensis*: 88%, n = 16, *L. triangularis*: 98%, n = 124). The guarding period can extend over a considerable period, in *L. triangularis* the longest guarding duration, i.e. the period of continuous presence of males in a female's web, was 12 days and the mean guarding duration was 4 ± 2,2 days (n = 63). In *L. triangularis* where sufficiently large sample sizes are available for the whole observation period males are present only in few webs of subadult females more than 10 days before their moult. The percentage of webs with males subsequently increases continuously until the day of the moult. Copulations usually take place immediately after the females' moults (*L. triangularis*: 90% within 1 h, n = 20). After the moult the percentage of webs with males drops to a low level.

MALE FIGHTING BEHAVIOUR

Due to the observed male visitation rates in webs of subadult females of 0,2 ± 0,30 males/h in *L. hortensis* (n = 180 web hours) and of 0,1 ± 0,28 males/h in *L. triangularis* (n = 277 web hours), guarding males are often confronted with intruding males. These conflicts are usually settled in the form of intensive fights as has been

previously described for *L triangularis* by ROVNER (1968). The two species differed remarkably with respect to the duration and intensity of the fights. In *L. hortensis* the mean duration of fights (n = 68) was 10 ± 25,5 s, many fights were ended after a vibrational threat display without physical contact of the males (38%) and no male was injured during these fights. In *L. triangularis* the fights (n = 61) were considerably longer (mean duration 101 ± 170,6 s), they escalated usually to physical fighting (77% of the fights) and often males were seriously injured or even killed in these fights (15% of the fights).

COPULATORY BEHAVIOUR

In *L. hortensis* there was a considerable remating probability of females in the lab (39%, n = 340) and the mean fertilization rate of second males was about 12 ± 19,6% (n = 60, range 0–85%) of the females eggs. In *L. triangularis* the remating probability was small (10%, n = 94) and in most (8 of 9) of the few cases where a remating took place the first copulation of the females was obviously anomalous, e.g. the first male only used one pedipalpus or the intromissions of the first male were incomplete.

After a complete copulation in the copulatory openings of *L. triangularis* females a solid mass of a whitish substance is visible. This mass is firmly attached to the openings for the rest of the females lifespans.

DISCUSSION

The spatial and temporal availability of mates is a very important factor influencing the evolution of a mating system: if males and females reach adulthood at different times or with different rates the result will often be an intense competition between members of the more abundant sex (mostly males) for members of the rarer sex (ANDERSSON 1994). In both *Linyphia*-species most males are mature considerable time before the first females moult and become receptive. So even considering a presumably greater mortality of wandering males (AUSTAD 1984), at every time of the reproductive period the operational sex ratio is strongly male biased and therefore a very intensive intrasexual competition between males for receptive females is to be expected.

In most araneomorph spider species the morphology of the female spermathecae with clearly separated copulation and fertilization ducts favours sperm precedence of first males (conduit spermathecae, AUSTAD 1984): the sperm of males that copulate first should fertilize all or at least a larger part of the eggs than sperm of later copulating males. Studies of the fertilization success of second males have confirmed this sperm priority pattern in Linyphiid spiders (*Frontinella pyramitela* (AUSTAD 1982), *Linyphia litigiosa* (WATSON 1990), *Linyphia hortensis* (this study). According to this sperm usage pattern males can optimize their reproductive success by copulating with virgin females. As has been shown by JACKSON (1986) males of many spider species guard subadult females until they moult and try to copulate imme-

diately after the females' moult. In both *Linyphia*-species such a precopulatory mate guarding (PARKER 1974*a*) is the prevailing behavioural strategy males use to gain access to virgin females. Almost all of the females are guarded at the day of their moult and most of the observed copulations took place immediately after the moult. The mate guarding behaviour of *L. triangularis* has been previously investigated by TOFT (1989) in a population in Denmark where the guarding rate was lower than in the present study. So this behavioural trait may be subject to inter-population variation according to population- or site-specific factors like web density or mortality of wandering males.

In species where copulation and fertilization are separated in time and females copulate more than once there may be sperm competition between the males copulating with a female (PARKER 1970). So the number of female matings is another important variable in the mating pattern of a species. Although the mating systems of the two *Linyphia* species are very similar in some aspects they differ remarkably in others. Females of *L. hortensis* are able to mate more than once and are apparently willing to do so. Second males can fertilize at least a part of the eggs of a female in this species. Thus there is a potential for sperm competition in *L. hortensis*. By contrast, *L. triangularis* females usually mate only once and males probably avoid sperm competition by closing the copulatory openings of the females with mating plugs after the copulation which probably make these openings inaccessible to following males. In *Agelena limbata* complete plugs lead to 100% sperm priority of first males (MASUMOTO 1993). Whether the completion of the copulation or the presence of the plug is responsible for the change to avoidance behaviour in *L. triangularis*-females can not be told at the moment.

The periods during which receptive females are present in the respective population therefore differ remarkably: it is longer in *L. hortensis* where the moulting period of females is long and even females which have copulated before may remain receptive. In *L. triangularis* it is shorter because the moulting period of females is short and only virgin females are receptive.

Thus, because virgin females in *L. triangularis* are available only for a short period and because males of this species usually avoid sperm competition by sealing the copulatory openings of the females after the copulation, virgin females should be more valuable to males in *L. triangularis* than in *L. hortensis*. This different reproductive value of virgin females for males is probably responsible for the remarkably different fighting behaviour during the guarding period: males of *L. triangularis* invest more energy and take greater risks in defending subadult females against rivals than males of *L. hortensis*. The result of this inter-specific comparison agrees well with the theory of fighting behaviour by PARKER (1974*b*) who postulated that males should adjust their fighting investments to the gain that can be expected.

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The fine structure of the spermatheca of *Pardosa lugubris* (Walckenaer, 1802)

Marika SUHM & Gerd ALBERTI
Institute of Zoology I, Im Neuenheimer Feld 230, D-69120 Heidelberg, Germany.

The fine structure of the spermatheca of *Pardosa lugubris* (Walckenaer, 1802). - The present paper is concerned with the structure of the spermatheca of *Pardosa lugubris*. Different types of pores have been found in the cuticle of the spermatheca. In the spermathecal epithelium we observed distinct cell complexes consisting of secretory and auxiliary cells with a cuticular ductule in its centre, which are leading to so-called primary pores. These pores are suggested as a primitive character in all spider species. A single porous plate located on the spermathecal stalk to which glandular cells lead, might be homologous to the dictynoid pores described by BENNETT (1992) and to the secondary pores observed in *Amaurobius fenestralis* (SUHM & ALBERTI 1993). We found secretion of some material into the spermathecal lumen through the primary and secondary pores. The biological function(s) of this secretion remain unclear, but it may play an important role in sperm maturation, nutrition and displacement.

Key-words: *Pardosa lugubris* - female genitalia - spermatheca - glandular epithelium - primary pore - secondary pore.

INTRODUCTION

Detailed observations on the structure of the secondary copulatory organs of spiders are not only of taxonomic, but also of functional and evolutionary importance. Despite of the necessity for comparative studies, there is only a small number of recent investigations that have provided information on the fine structure of female genitalia in spiders (LOPEZ & JUBERTHIE-JUPEAU 1983; SUHM & ALBERTI 1993; UHL 1994). Therefore, we studied the fine structure of the spermatheca of *Pardosa lugubris* with its surrounding epithelium by means of light, scanning and transmission electron microscopy.

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MATERIALS AND METHODS

Pardosa lugubris (Walckenaer, 1802) specimens were collected near Heidelberg, Germany. For light (LM) and transmission electron microscopic (TEM) studies, the surrounding tissues were excised and fixed in ice cold 2.5% glutaraldehyde buffered in 0.1 M sodium cacodylate (pH 7.6) for two hours, rinsed again in buffer and postfixed for 2 hours in 1% osmium ferrocyanide (Karnovsky 1971). After washing in 0.1 M cacodylate and 0.05 M maleate buffer (pH 5.2), tissues were stained en bloc with 1% uranyl acetate in maleate buffer for 1 hour. Specimens were dehydrated in a graded series of ethanol and embedded in Spurr's medium (Spurr 1969). Semithin sections were stained with methylene blue-azur II (Richardson 1960) and examined in a Leitz Aristoplan microscope. Ultrathin sections were stained with alkaline lead citrate (Reynolds 1963) for 30–60 s and examined in a Zeiss EM 9. For scanning electron microscopic (SEM) studies the female copulatory organ was cleaned with lactic acid for 5–10 minutes before dehydrated in alcohol and sputtercoated with gold in a Technics-Hummer I sputter and examined in a Philips SEM 505. To expand the male palpal organs they were incubated in hot lactic acid.

RESULTS

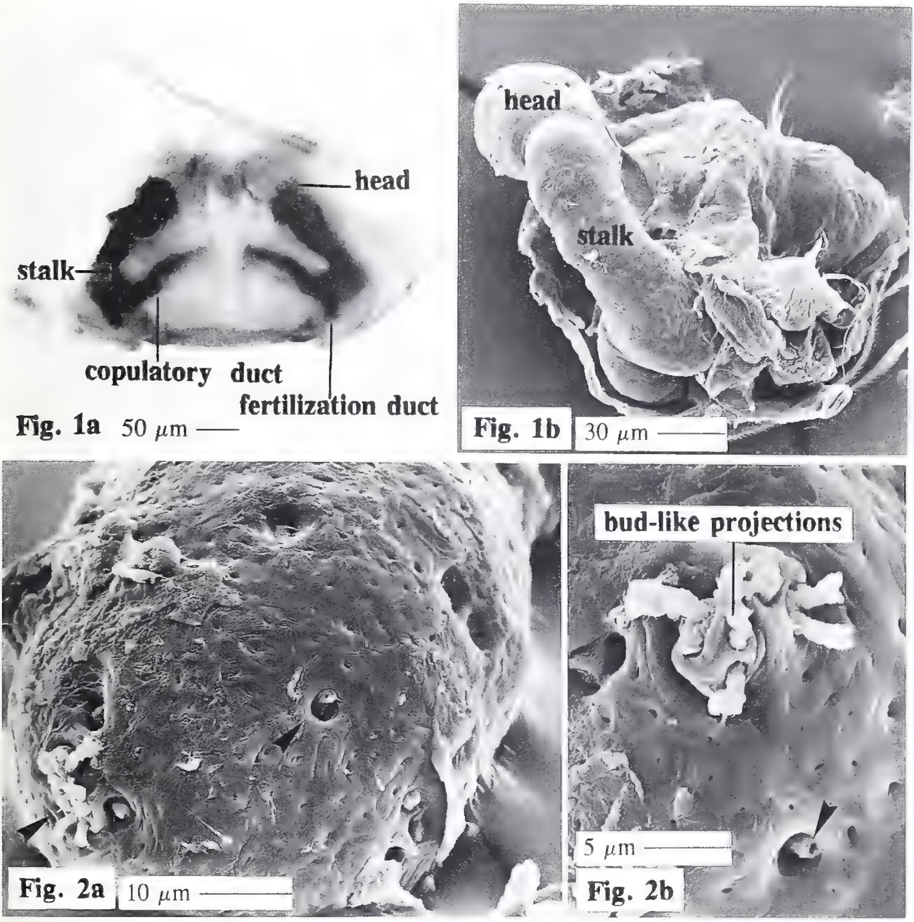
The female genitalia of *Pardosa lugubris* are of the entelegyne type. In this spider species each spermatheca is elongated and consists of a stalk region and a blind ending head of the spermatheca which is slightly dilated. The copulatory opening leads via the short, thick-walled copulatory duct into the stalk region of the spermatheca, from where the short fertilization duct arises to the posterior end of the epigynal fold leading into the uterus externus (Figs. 1a, 1b).

The cleared epithelial side of the spermathecal cuticle exhibits approximately 20 more or less evenly distributed complex pores (primary pores), restricted to the head of the spermatheca. In *P. lugubris* most of the primary pores are cavities penetrated by 1–2 cuticular ductules, whereas few of the primary pores form bud-like projections with 3 or more ductules (Figs. 2a, 2b).

Our ultrastructural studies on the spermathecal epithelium shows two ectodermal glands separated from the haemolymph by a basement membrane. One gland consists of type III gland units, whereas the other gland consists of type I gland cells according to the classification of Noirot & Quennedy (1974, 1991).

Each type III gland unit is composed of several cell types: The prominent secretory cells exhibit a basal labyrinth. The cytoplasm contains mitochondria, well developed Golgi regions and rough endoplasmic reticulum filled with large amounts of some fibrous material (Fig. 3). The microvilli of several secretory cells (Fig. 4) project into a common lumen which terminates in a cuticular ductule leading to a primary pore.

Once we observed two ciliary structures of the 9X2+0 axonemal pattern within the proximal part of the ductule (Fig. 5). The ductule is surrounded by a canal cell. The secretory cell as well as the canal cell are surrounded by several narrow sheath

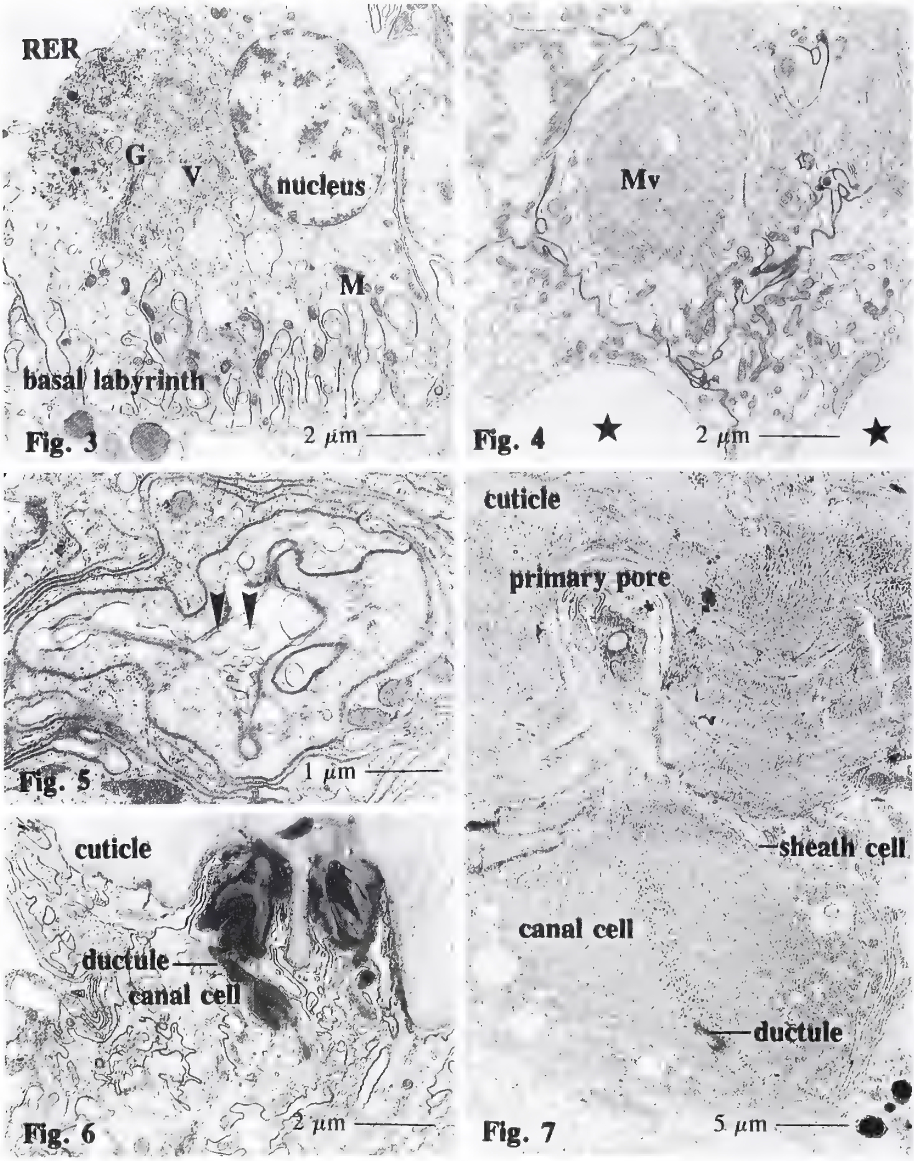


FIGS 1–2

Fig. 1a. Dorsal view of the vulva. The copulatory and fertilization duct lead into the stalk region of the spermatheca, which leads into the slightly dilated head of the spermatheca. Fig. 1b. SEM on the spermathecal stalk and the head of the spermatheca. Fig. 2a. Overview of the cleared epithelial side of the head of the spermatheca. (Pores indicated). Fig. 2b. Higher magnification. Primary pores as "simple" cavities with cuticular ductules (arrow) or bud-like projections with several ductules.

cells. Their cytoplasm is electron lucid and only few organelles were observed. In contrast to the secretory cells, the nuclei of the sheath cells are not located basally, but more apically near the cuticular ductule. The canal and sheath cells convey the cuticular ductule into the primary pore (Figs. 6, 7).

Furthermore, a single secondary pore is located on the spermathecal stalk which is not detectable by the scanning electron microscope, but by light and



FIGS 3–7

Fig. 3. A secretory cell showing a basal labyrinth. The cytoplasm contains rough endoplasmic reticulum (RER), filled with some fibrous material, mitochondria (M) and well developed Golgi region (G). V Golgi vesicles. Fig. 4. Several secretory cells which project microvilli (Mv) into a common lumen. Prominent RER cisternae are filled with fibrous material (asterisk). Fig. 5. Proximal part of the ductule surrounded by a canal cell. Ciliary structures of the 9X2+0 axonemal pattern within the lumen (arrows). Fig. 6. Canal cell conveying the cuticular ductuleinto the primary pore. Fig. 7. Canal and sheath cells leading into the primary pore.

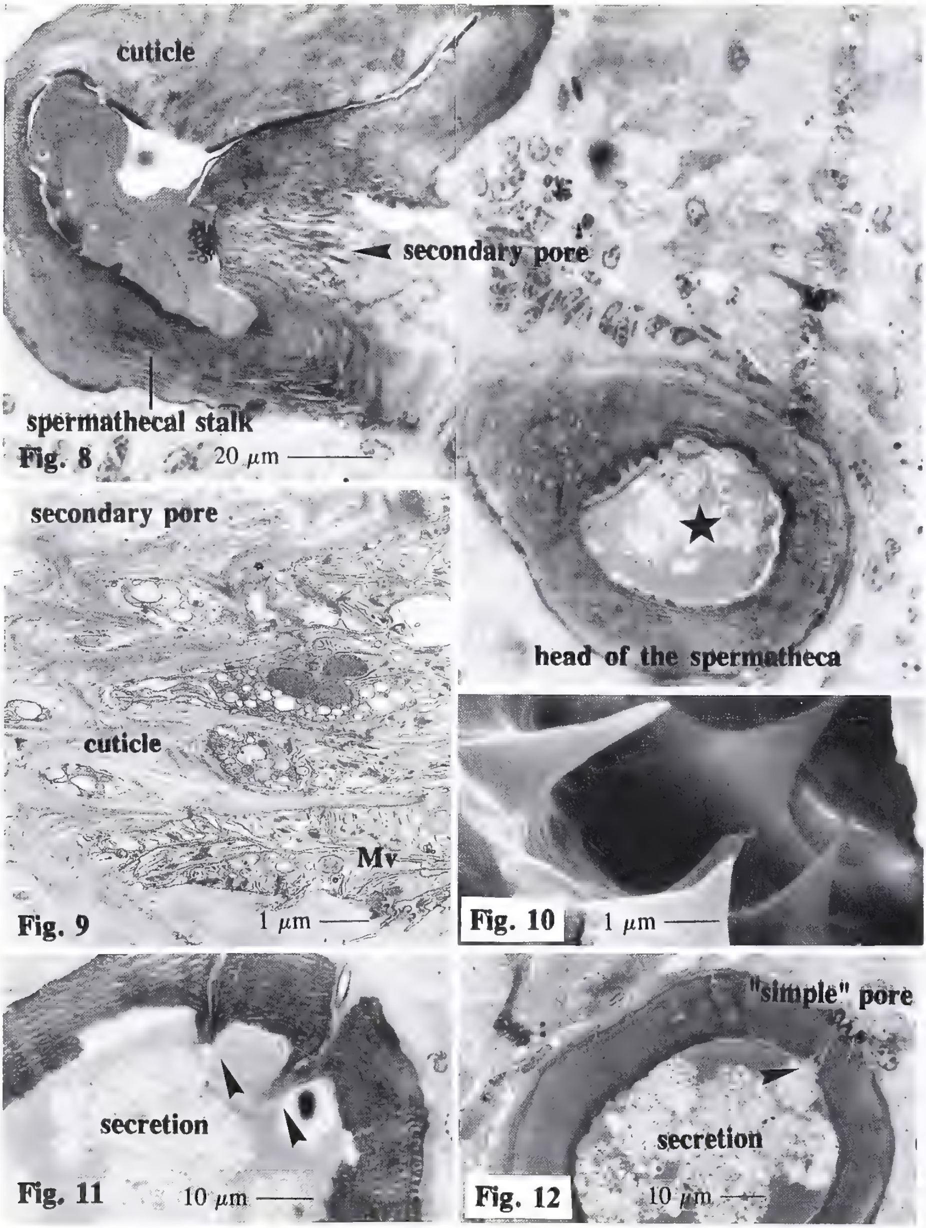
transmission microscopy as it is hidden by the copulatory duct. The secondary pore is plain and therefore does not extend into the lumen of the stalk (Fig. 8). The cell processes of the second gland already mentioned lead to this porous plate. The gland is built up by a single cell type: The nuclei are located basally and are of elliptic shape. In this region, we found also mitochondria, rough endoplasmic reticulum and Golgi regions. Apically the cells narrow and their microvilli penetrate the perforated cuticle of the spermathecal stalk (Fig. 9). The spermathecal epithelium is only sparsely innervated.

The luminal cuticular spermathecal surface shows distinct projections, too. The basal part of the stalk region exhibits many solid thornlike projections (Fig. 10). In contrast, in the head of the spermatheca some few primary pores end within cannular, hollow cuticle projections (Fig. 11), whereas most other primary pores are "simple" pores through which exudation into the lumen occurs (Fig. 12).

DISCUSSION

Perforations similar to primary pores have been described in many spider species. They occur in haplogynes (Cook 1966; Brignoli 1976; Coyle *et al.* 1983) as well as in entelegynes (Strand 1906; Sierwald 1989; Bennett 1992). Observations of the fine structure of primary pores of *Segestria senoculata* (Linné, 1758) (Segestriidae) (unpubl.), *Antrodiaetus unicolor* (Hentz, 1842) (Antrodiaetidae) (unpubl.), *Pholcus phalangioides* Fuesslin, 1775 (Pholcidae) (Uhl 1994) and *Amaurobius fenestralis* (Stroem, 1768) (Amaurobiidae) (Suhm & Alberti 1993) have shown a structure similar to that of *Pardosa*. This study provides further support for the hypothesis of primitive presence of primary pores in the vulva of all spiders as suggested by Sierwald (1989). The occurrence of further, complex pores restricted to the stalk region has only been reported in few spider species, which are all of the entelegyne type. In the spermatheca of *Agelena labyrinthica* (Clerck, 1757) (Agelenidae), Strand (1906) described a single perforation resembling that of *A. fenestralis* recorded by Suhm & Alberti (1993). There is also an obvious similarity in the fine structure of the secondary pore of *A. fenestralis* located within a concavity and the porous plate of *Pardosa lugubris*, because both are located in the stalk region and show a similar fine structure. Therefore, these structures might be homologous. Bennett (1992) described single pores in the stalk region as synapomorphic for dictynoid spiders (referring to Amaurobioidea, Dictynoidea sensu Platnick 1989), hence he termed them dictynoid pores. Although Bennett supposed no "dictynoid" pores for lycosids and *Amaurobius*, we found pores in the stalk region in both of them. As most studies on the female genitalia are SEM studies, the porous plate might not have been detected, since it is possibly hidden by the copulatory or fertilization duct as it is in *P. lugubris*. Therefore, this pore may be more generally distributed than suggested by Bennett. In our opinion the secondary pore needs to be reevaluated as a taxononic character state for dictynoid spiders.

Primary pores have been regarded as glandular ductules. However, as we already described in *A. fenestralis* (Suhm & Alberti 1993) we also found some



Figs 8–12

Fig. 8. LM study on the spermatheca shows the porous plate (secondary pore; arrow). The head of the spermatheca is filled with some material (asterisk). Fig. 9. The narrow apical cell regions of the secondary pore gland show microvilli (Mv) leading to the pore. Fig. 10. SEM showing solid thornlike projections in the lumen of the basal part of the stalk region. Fig. 11. Cannular cuticle projections (arrows) protruding into the lumen of the head of the spermatheca. Fig. 12. "Simple" pores in the cuticle of the head of the spermatheca through which exudation of some material appears (arrow).

similarities to typical arthropod sensilla like: ciliary structures (receptor cells?), several auxiliary cells (canal and sheath cells) and a cuticular ductule that may correspond to the dendritic sheath.

In the case of *P. lugubris* ciliary structures within the glandular duct were found only once. Furthermore, the epithelium does not seem to be strongly innervated. Therefore, it might be possible that most of the primary pores function as ectodermal glands, whereas only few other pores may have another/additional function. The cannular projections found in the lumen of the head of the spermatheca may allow a better mixing of the secretion with the sperm mass, whereas the solid thornlike structures observed in the stalk region might retain the sperm mass within the spermatheca as OSTERLOH (1922) suggested in *Pardosa amentata* (Clerck, 1757). The glandular cells leading to the secondary pore seem to exude some product into the spermathecal lumen, too. The function of the two ectodermal glands found in *Pardosa* remains unclear, but their secretion might contribute directly to sperm nutrition, activation and/or move the sperm from the receptaculum into the fertilization duct prior to oviposition as already suggested by many other authors. Unfortunately none of the substances were isolated for chemical or biological characterization, and without additional information, their precise contribution to reproduction must remain unsolved.

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Preliminary results on foliage-dwelling spiders on black pine (*Pinus nigra*) by beating on 5 sites in Hungary

Csaba SZINETÁR
Department of Zoology Berzsenyi College, Károlyi Gáspár tér 4,
H-9701 Szombathely, Hungary

Preliminary results on foliage-dwelling spiders on black pine *(Pinus nigra)* **by beating on 5 sites in Hungary.** - The surveying of foliage-dwelling spiders was carried out at 5 different study-sites in Hungary. The samples were made with beating net. The total number of 2102 spider specimens belonged to at least 71 species. In the studied towns the density and the species diversity of the spider community were lower in the town centres than in the suburbs.

Key-words: foliage-dwelling spiders - black pine - density - species diversity.

INTRODUCTION

Though all spiders are predatory, plants play on outstanding role in the life of many of them. It is a well known and characteristic fact about nearly all plant dwelling spiders which plants they prefer in their habitat selection. Many studies deal with foliage-dwelling spiders of evergreen coniferous trees, too (BALOGH 1935, KOLOSVARY 1933, 1935, JENNINGS 1987, GUNNARSSON 1988, MASON 1992, SZINETAR 1992, KNOFLACH & BERTRANDI 1993, SIMON 1995).

The black pine (*Pinus nigra* spp. *nigra*) occurs in Central Europe, from Austria to Central Italy and to Greece (MEUSEL *et al.* 1965). In Hungary, it is planted in different arid and dry biotopes and in towns.

Through the examination of five collecting spots (Map 1), we tried to find answers to the following questions:

1. What species can be found on foliage of black pine?
2. Which are the most typical accompanying species of black pine?
3. Are there differences in the characteristics of the spider fauna in different parts of the country, as well as between the biotops of city-centres and outskirts, and biotops with different environmental loading?

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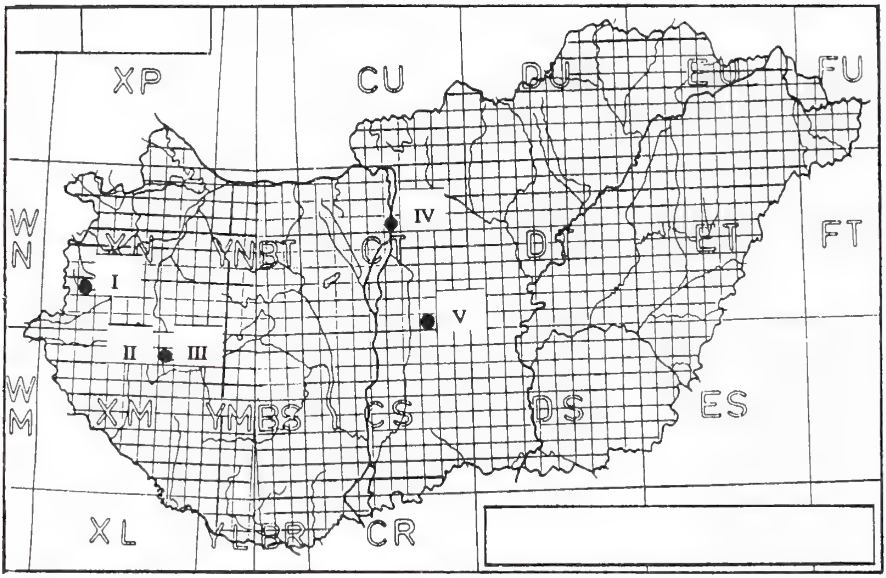

Fig. 1

The study sites in Hungary. I. Szombathely; II. Keszthely; III. Balatongyörök; IV. Budapest; V. Fülöpháza.

MATERIALS AND METHODS

The samples were taken with beating net from foliage 1,5–2 metres high. Ten 70 cm long branches constituted one sampling unit. The density values were calculated on the basis of the ten 70 cm long branches: number of spiders per ten branches.

The index of species abundance (S.ISA) using Kendall's rank-correlation method (Kendall 1962) has been examined, which, besides the number of individuals of the species considers the number of the sites where the species was found, as well as the position the species occupied in the rank of precedence in some collecting areas.

In a few cases the density and species diversity of the foliage-dwelling spiders have been compared between the city-centres and the suburban areas, as well as the industrial area and the suburbs with gardens. Delete-one jackknifed form of the Shannon-Wiener estimates were calculated (Adams & McCune 1979). The significance of diversity differences has been tested by an adequate version of the t-test (Izsak 1994).

The samples was carried out in five different study sites in Hungary. The sampling times weren't same ones during the summer season therefore the possibility of comparison between the sites can be restricted.

I. Szombathely (UTM:XN23) urban biotops in a major town in Western Hungary (23 June to 01 July 1994);

II. Keszthely (UTM:XM78) urban biotops in a little central Transdanubian town (24 June, 30 June, 10 August 1994);

III. Balatongyörök (UTM:XM78) black pine stand planted in the area of a recultivated dolomite quarry (10 July 1994);

IV. Budapest (UTM:CT56) Sas-hill, Nature Protection area, black pine stand planted in original dolomitic vegetation (21 June 1994, 25 May, 21 June, 15 August 1995);

V. Fülöpháza (UTM:CS89) Kiskunság National Park, black pine stand planted in calciferous sandy-soil (05 May 1993, 18 May 1994, 17 May 1995).

RESULTS

The total number of 2102 spider specimens (255 females, 106 males, 1741 juveniles) belonged to at least 71 species (Table 1).

The species found most frequently can be seen in Table 3. These 10 species comprise 52% of the whole sample.

In Szombathely, the density of samples taken in the centre and in the suburbs showed significant differences (Suburb: d = 60±27.024 specimens/10 branches, city: 22.25±7.65, $t_8 = 3.80$, The t values was significant at the 1% probability level.).

In Keszthely, at the crossroads in the industrial district of the town, the species diversity of the foliage-dwelling spiders (IV) was significantly lower than that of on the trees of the garden-area (I, II) or in the areas out of the town (III).

Particularly, the jackknifed diversity values and the results of the significancy tests are given in Table 2. All of the t values are significant at the 5% probability level.

DISCUSSION

It can be said on the base of the data of the five sample sites, that black pine offers good conditions for settling down for numerous spiders even in busy town areas.

Despite its uniformity, the spider fauna shows some local characteristics. From the neighbouring habitats, some species that are characteristic of the given geographical area or some adjoining habitats immigrate in a low number of individuals. Accordingly, for example, in the city-centre of Szombathely, *Dictyna civica* from the walls of houses; in Keszthely *Gongylidiellum murcidum* from the neighbouring reeds; in Fülöpháza *Argiope lobata* and *Uloborus walckenarius* from sandy grassland, in Budapest *Sintula spinigera* from the dolomitic vegetation can be the species which were found accidentally.

The examination of spiders dwelling on the foliage of black pine as a special habitat – whose structure, in addition, is permanent – may offer possibility in the future to obtain information on the area surrounding the concrete biotop under research (e.g. geographical location, environmental loading).

TABLE 1

Number of foliage-dwelling spiders collected on *Pinus nigra* in Hungary (females/males (juveniles)) I. Szombathely; II. Keszthely; III. Balatongyörök; IV. Budapest; V. Fülöpháza.

Species	I	II	III	IV	V	Σ
Dysderidae						
Harpactea rubicunda (C.L. Koch, 1838)	–/–	–/–	1/–	–/–	–/–(1)	1/–(1)
Segestriidae						
Segestria bavarica C.L. Koch, 1843	–/–(1)	–/–(3)	–/–(1)	–/–	–/–	–/–(5)
Uloboridae						
Hyptiotes paradoxus (C.L. Koch, 1834)	–/–(3)	–/1(1)	–/–(2)	–/–	–/–	–/1(6)
Uloborus walckenarius Latreille, 1806	–/–	–/–	–/–	–/–	–/–(1)	–/–(1)
Tetragnathidae						
Tetragnatha obtusa C.L. Koch, 1837	–/–	–/1	–/–	–/–	–/–	–/1
Tetragnatha spp. juv.	–/–(6)	–/–(39)	–/–	–/–	–/–	–/–(45)
Araneidae						
Agalenatea redii (Scopoli, 1763)	–/–	–/–	–/–	–/–	2/–	2/–
Araneus diadematus Clerck, 1757	–/–(5)	1/2(44)	–/–(9)	–/–(4)	–/–	1/2(62)
Araniella cucurbitina (Clerck, 1757)	1/–	–/–	–/1	1/–	10/4	12/5
Araniella spp. juv.	–/–(1)	–/–(4)	–/–(3)	–/–(1)	–/–(14)	–/–(23)
Argiope lobata Pallas, 1772	–/–	–/–	–/–	–/–	–/–(3)	–/–(3)
Atea sturmi (Hahn, 1831)	–/–	–/1	–/–	–/–	–/–	–/1
Atea sp. juv.	–/–(11)	–/–(26)	–/–(1)	–/–	–/–	–/–(38)
Gibbaranea bituberculata (Walckenaer, 1802)	–/–	–/–	–/–	–/–	2/–	2/–
Gibbaranea omoeda (Thorell, 1870)	1/–	–/–	–/–	–/–	–/–	1/–
Gibbaranea sp. juv.	–/–(2)	–/–	–/–(2)	–/–	–/–	–/–(4)
Mangora acalypha (Walckenaer, 1802)	–/–	–/–(8)	–/–	–/–(3)	4/4(9)	4/4(20)
Zilla diodia (Walckenaer, 1802)	–/–	–/–	–/–	–/–(2)	–/–	–/–(2)
Araneidae spp. juv.	–/–(82)	–/–(20)	–/–(78)	–/–(9)	–/–(51)	–/–(240)
Mimetidae						
Ero aphana (Walckenaer, 1802)	1/–	–/–(1)	–/–	–/–	–/–	1/–(1)
Linyphiidae						
Gongylidiellum murcidum Simon, 1884	–/–	–/1	–/–	–/–	–/–	–/1
Lepthyphantes tenuis (Blackwall, 1852)	1/–	–/–	–/–	1/–	–/–	2/–
Linyphia triangularis (Clerck, 1757)	–/–	1/2	–/–	–/–	–/–	1/2
Linyphia frutetorum (C.L. Koch, 1834)	–/–	–/–	1/–	1/–	3/–	5/–
Meioneta rurestris (C.L. Koch, 1836)	1/–	–/–	–/–	1/–	1/–	3/–
Porrhomma microphthalmum (0.P.-Cambridge, 1871)	–/–	–/–	–/–	1/–	–/–	1/–
Sintula spinigera (Balogh, 1935)	–/–	–/–	–/–	1/–	–/–	1/–
Linyphiinae spp. juv.	–/–(46)	–/–(4)	–/–(44)	–/–(59)	–/–(52)	–/–(205)
Theridiidae						
Anelosimus vittatus (C.L. Koch, 1836)	3/–	–/–	–/–	–/–	–/–	3/–
Dipoena melanogaster (C.L. Koch, 1845)	1/–	1/–	1/–	2/–(7)	1/7(19)	6/7(26)
Enoplognatha lineata (Clerck, 1757)	–/1	–/–	–/–	–/–	–/–	–/1
Enoplognatha sp. juv.	–/–	–/–	–/–(1)	–/–(1)	–/–	–/–(2)
Episinus angulatus (Blackwall, 1836)	–/–	–/–	–/1	–/–	–/–	–/1
Episinus sp. juv.	–/–	–/–	–/–(3)	–/–	–/–(2)	–/–(5)
Neottiura bimaculata (Linné, 1767)	–/–	–/–	–/–	–/–(1)	–/–(2)	–/–(3)
Steatoda bipunctata (linné, 1758)	–/–(1)	–/1	–/–	–/–	–/–(1)	–/1(2)
Theridion sisyphium (Clerck, 1757)	–/–	–/–	–/–	–/1	–/–	–/1
Theridion impressum L. Koch, 1881	1/–	–/–	–/–	–/–	–/–	1/–
Theridion (*sisyphium, impressum* juv.)	–/–(5)	–/–(1)	–/–	–/–(23)	–/–(9)	–/–(38)
Theridion mystaceum L. Koch, 1870	3/–	3/–	–/–	–/–	–/–	6/–
Theridion nigrovariegatum Simon, 1873	–/–	–/–	–/–	3/1(1)	–/–	3/1(1)
Theridion pallens Blackwall, 1834	–/–	–/–	1/–	–/–	–/–	1/–
Theridion pinastri C.L. Koch, 1872	6/4	3/2	5/1	3/1(1)	–/–(6)	17/8(7)
Theridion simile C.L. Koch, 1836	–/–	–/–	–/–	–/–	1/2(1)	1/2(1)

Theridion tinctum (Walckenaer, 1802)	6/–(1)	22/3(25)	5/2	–/–	–/2(33)	33/7(59)
Theridion varians Hahn, 1833	3/–	1/–	–/–	–/–	–/–	4/–
Theridion spp. juv.	–/–(51)	–/–(1)	–/–(6)	–/–(10)	–/–(7)	–/–(75)
Oxyopidae						
Oxyopes sp. juv.	–/–	–/–	–/–	–/–	–/–(4)	–/–(4)
Agelenidae						
Agelena gracilens C.L. Koch, 1841	–/–(5)	–/–	–/–	–/–	–/–	–/–(5)
Dictynidae						
Dictyna civica (Lucas, 1849)	3/2	–/–	–/–	–/–	–/–	3/2
Dictyna pusilla Thorell, 1856	4/–	–/–	–/–	–/–	–/–	4/–
Lathys humilis Blackwall, 1855	10/–	2/–	–/–	–/–	1/–	13/–
Dictyna spp. juv.	–/–(3)	–/–	–/–	–/–	–/–	–/–(3)
Lathys puta (O.P.-Cambridge, 1863)	–/–	1/–	–/–	–/–	–/–	1/–
Lathys spp. juv.	–/–(24)	–/–(5)	–/–(1)	–/–	–/–	–/–(30)
Anyphaenidae						
Anyphaena accentuata (Walckenaer, 1802)	–/–(2)	–/–	–/–(1)	–/–	2/2	2/2(3)
Clubionidae						
Cheiracanthium mildei L. Koch, 1864	–/–	–/–	–/–	–/1	–/–	–/1
Cheiracanthium sp. juv.	–/–(1)	–/–(7)	–/–	–/–(14)	–/–	–/–(22)
Clubiona genevensis L. Koch, 1867	10/–(35)	4/–(35)	–/–	4/–(4)	12/1(4)	30/1(78)
Clubiona spp. juv.	–/–(27)	–/–(11)	–/–	–/–(2)	–/–	–/–(40)
Gnaphosidae						
Callilepis nocturna (Linné, 1758)	–/–	–/–	–/–	–/–	–/1	–/1
Micaria sp. juv.	–/–(1)	–/–	–/–	–/–	–/–	–/–(1)
Scotophaeus blackwalli (Thorell, 1871)	–/–	–/–	–/–	1/–	–/–	1/–
Scotophaeus scutulatus (L. Koch, 1866)	1/–	–/–	–/–	–/–	–/–	1/–
Scotophaeus spp. juv.	–/–	–/–	–/–	–/–(1)	–/–	–/–(1)
Zelotes sp. juv.	–/–	–/–	–/–	–/–(1)	–/–	–/–(1)
Philodromidae						
Philodromus aureolus (Clerck, 1757)	–/–	–/–	–/–	–/1	–/1	–/2
Philodromus cespitum (Walckenaer, 1802)	2/4	–/–	–/–	2/2	–/–	4/6
Philodromus collinus C.L. Koch, 1835	–/3	1/–	1/–	–/–	–/–	2/3
Philodromus margaritatus (Clerck, 1757)	1/–	–/–	–/–	–/–	2/–	3/–
Philodromus praedatus (O.P.-Cambridge)	–/1	–/–	–/–	–/–	–/–	–/1
Philodromus spp. juv.	–/–(198)	–/–(59)	–/–(51)	–/–(92)	–/–(53)	–/–(453)
Tibellus sp. juv.	–/–	–/–	–/–	–/–(1)	–/–	–/–(1)
Thomisidae						
Heriaeus mellottei Simon, 1866	–/–	–/–	–/–	1/2	–/–	1/2
Misumena vatia (Clerck, 1757)	–/–	–/–	–/–	–/–	–/–(1)	–/–(1)
Tmarus piger (Walckenaer, 1802)	–/–	–/–(1)	–/–	–/–	–/–(1)	–/–(2)
Xysticus spp. juv.	–/–(19)	–/–(6)	–/–(9)	–/–(20)	–/–	–/–(54)
Salticidae						
Dendryphantes rudis (Sundevall, 1832)	–/–	4/–(11)	–/–	–/–	5/1(11)	9/1(22)
Eris nidicolens (Walckenaer, 1802)	15/7(22)	6/2(37)	5/–(6)	7/1(13)	6/10(10)	39/20(88)
Euophrys obsoleata (Simon)	–/–	–/–	1/–	–/–	–/–	1/–
Euophrys sp. juv.	–/–	–/–	–/–(2)	–/–	–/–	–/–(2)
Evarcha falcata (Clerck, 1757)	–/–	–/–	–/–	–/–	1/–	1/–
Heliophanus cupreus (Walckenaer, 1802)	–/–	–/–	–/–	–/–	2/–	2/–
Heliophanus spp. juv.	–/–	–/–	–/–	–/–(19)	–/–	–/–(19)
Marpissa muscosa (Clerck, 1757)	–/–	–/–(1)	–/–	–/–	2/–(7)	2/–(8)
Philaeus chrysops (Poda, 1761)	–/–	–/–	–/–	–/–(1)	–/–	–/–(1)
Salticus scenicus (Clerck, 1757)	–/–	–/–	–/–	–/–	–/1	–/1
Salticus zebraneus (C.L. Koch, 1837)	6/2	8/7	8/–	2/2	–/8	24/19
Salticus spp. juv.	–/–(2)	–/–(8)	–/–(7)	–/–(5)	–/–(3)	–/–(25)
	80/24(554)	58/23(358)	29/5(227)	31/12(295)	57/42(307)	2102

TABLE 2

Jackknifed estimates (J) of the Shannon-Wiener indices. The t statistics relate to the differences between the J values belonging to the areas and to the industrial district, respectively (Keszthely).

	J	t
I. garden area # 1	2.7740	4.270
II. garden area # 2	2.7557	4.779
III. areas out of the town	2.5445	2.559
IV. industrial district	2.1589	–

TABLE 3

The 10 most abundant spider species/genera on *Pinus nigra* (S.ISA KENDALL 1962).

		S. ISA
1.	*Philodromus* spp. juv.	1
2.	*Eris nidicolens*	0.94
3.	*Salticus zebraneus*	0.85
4.	*Theridion tinctum*	0.77
5.	*Theridion pinastri*	0.76
6.	*Clubiona genevensis*	0.71
7.	*Araniella cucurbitina*	0.65
8.	*Araneus diadematus*	0.64
9.	*Theridion (sisyphium, impressum)* juv.	0.55
10.	*Dipoena melanogaster*	0.51

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Stridulation in *Palpimanus gibbulus* Dufour (Araneae: Palpimanidae)

Gabriele UHL *
Albert-Ludwigs-Universität
Institut für Biologie I (Zoologie)
Albertstrasse 21a, D - 79104 Freiburg i.Br., Germany
&
Michael SCHMITT
Zoologisches Forschungsinstitut und Museum Alexander Koenig
Adenauerallee 160, D - 53113 Bonn, Germany.

Stridulation in *Palpimanus gibbulus* Dufour (Araneae: Palpimanidae). - Individuals of *Palpimanus gibbulus* Dufour, 1820 from the Mediterranean islands of Naxos (Greece) and Sardinia (Italy) were found to stridulate when disturbed. The stridulatory organ belongs to the file-and-scraper type with the pars stridens on the outer face of the chelicera and the plectrum on the femur of the pedipalpus. The sounds are audible to the human ear from a very short distance only. They were recorded using an inductive transducer. The stridulatory signals were of a simple temporal structure, rather irregular and showed no marked frequency gaps. Power maxima were at 1.00 kHz and 2.42 kHz. Upper end of frequency range was at 8 kHz.
In *P. gibbulus* both sexes engage in sound production. Stridulation in *P. gibbulus* apparently serves at least a two-fold purpose: firstly, as a potential defence mechanism and secondly, in intraspecific communication. However, during courtship and mating, only males were clearly observed to stridulate.

Key-words: sound production - stridulation - communication - Palpimanidae - bioacoustics - morphology - courtship - behaviour.

INTRODUCTION

Sound production in spiders has been reported for 26 families (UETZ & STRATTON 1982) and various descriptions of morphological structures probably related to sound production indicate it may be even more widespread. The methods of

* present address: Biologisk Institut, Afdeling for Zoologi, Århus Universitet, Universitetsparken, Bygning 135, DK-8000 Århus C, Danmark.

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sound production are 1) stridulation (friction of rigid body parts), 2) percussion (striking the substratum) and, more rarely 3) vibration (oscillation of leg or body). Here, we focus exclusively on stridulation and refer those interested in other methods of sound production to UETZ & STRATTON (1982).

Although stridulation has been reported in 22 spider families (Uetz & Stratton 1982), only few studies have investigated the behavioural context in which it occurs, with the exception of the Theridiidae and Lycosidae (e.g. BRAUN 1956; GWINNER-HANKE 1970; STRATTON & UETZ 1983). Stridulation requires the movement of one body part (the plectrum or scraper) across a second body part (pars stridens or file). The location of file and scraper on the body of the spiders varies widely: there are 12 different types of mechanisms classified according to the location of the sound-producing structures (STARCK 1985, based on LEGENDRE 1963). It is assumed therefore that stridulation has evolved independently several times in spiders.

In the detailed surveys of LEGENDRE (1963) and STARCK (1985) the Palpimanidae are not listed as stridulating spiders, which is possibly due to the limited distribution and rare occurrence of the Palpimanidae. To our knowledge there is only little information on stridulation in this taxon: LAWRENCE (1962) named a *Palpimanus* species from the Namib desert *Palpimanus stridulans* and described its stridulatory organ morphologically. BRIGNOLI (1980) mentioned a stridulatory file on the chelicerae of an undetermined Palpimanus female from Sardinia but provided no further information on shape or structural details.

MATERIALS AND METHODS

The specimens examined belong to *Palpimanus gibbulus* Dufour, 1820. Although DUFOUR described the species as "*P. gibullus*", this is best regarded as a lapsus according to PLATNICK (1981). DUFOUR described the prosoma in Latin as hunch-backed ("thorace gibbo") which confirms the validity of the species name, *P. gibbulus*, used in the vast majority of citations.

P. gibbulus individuals were found in pine forests under stones or pieces of bark lying on the ground. The spiders were clinging to stones when these were picked up. Adults and juveniles of *P. gibbulus* were collected from Rhodos (Greece) in 1987, from the Cyclade island of Naxos (Greece) in 1990 and from Sardinia (Italy) in 1992, 1993 and 1994. Individuals from Sardinia were reared and kept in the laboratory in small plastic boxes containing a layer of gypsum and a piece of bark from their original locality. They were fed with nymphs and juveniles of the cellar spider *Pholcus phalangioides* (Fuesslin, 1775).

For morphological investigation 6 specimens preserved in ethanol from Naxos, Rhodos and Sardinia were dehydrated in a graded series of ethanol, critical-point dried, sputter-coated with gold and examined with a Zeiss Semco Nanolab 7 and a Hitachi S2460N SEM.

In order to investigate the behavioural context of stridulaton, the reaction of female and male *P. gibbulus* to disturbances (pinching, pushing) was observed.

Additionally, mating behaviour of 3 females and 2 males from Sardinia was studied. Males were brought to female boxes and behaviour was registered during the course of the following 2 hours. All individuals used for mating experiments were taken to the laboratory as adults. None of the juvenile individuals collected from the field reached maturity in the laboratory.

For bioacoustic investigations a light-weight magnet glued onto the spider's prosoma in combination with a magneto-dynamic vibration transducer was used (constructed by Th. Rollenhagen, Berlin: see Strubing & Rollenhagen 1988). Spiders were disturbed with tweezers to evoke defence stridulation which was recorded by a stereo tape recorder (Sony WM D6C). Sounds were visualized with a spectrum analyser (Spectro 2000, MEDAV) which produced an on-line Fast Fourier Transformation visible on a colour monitor. For further analysis, records were sampled into a computer (Tandon 486/33, Compaq) via an analog-digital converter (DT2821, Data Translation) and analysed with signal processing software (Hypersignal Acoustic, Hyperception Inc.).

RESULTS

Morphology

The stridulatory apparatus of *P. gibbulus* belongs to the chelicera-pedipalp type with the file situated laterally on the chelicera and the plectrum on the inner side of the pedipalp (fig. 1A). Both sexes possess a stridulatory apparatus. The morphology of the file appeared uniform in all individuals investigated, i.e. neither a sexual dimorphism nor differences between populations were apparent (figs. 1C, 1D). The stridulatory file extends 580 - 620 μm along the surface of the chelicera and consists of two areas, a proximal area (180 - 200 μm) the surface of which is undulated (figs. 1C, 1D) and consists of small parallel ribs (ca. 0.5 μm thick and 2 μm high) and a distal smooth area of larger parallel ribs (fig. 1B) which covers about 400 μm. These ribs are about 1μm wide at the top and around 3.5 μm at the base and 3 - 5 μm high.

The plectrum is situated on the pedipalp, i.e. on the inner lateral surface of the femur and is composed of several modified setal bases (fig. 2A). Figure 2C shows the arrangement of the plectrum: a row of bristles starts proximally on the femur and continues halfway along its longitudinal axis. The bases of the bristles are enlarged and sharp-edged (fig. 2B). The bases are 7 - 13 μm high and 7 - 10 μm broad. The plectra of the specimens from Rhodos appeared to be slightly smoother in shape, but the difference between populations was not marked. The morphology of the plectra is not sexually dimorphic.

Behaviour

When handling a live *P. gibbulus* female, one of us (GU) was alerted to the up and down movements of the spider's pedipalps. Movements of both palps were not in phase. Holding the spider close to the ear, a faint, high-pitched buzz was audible.

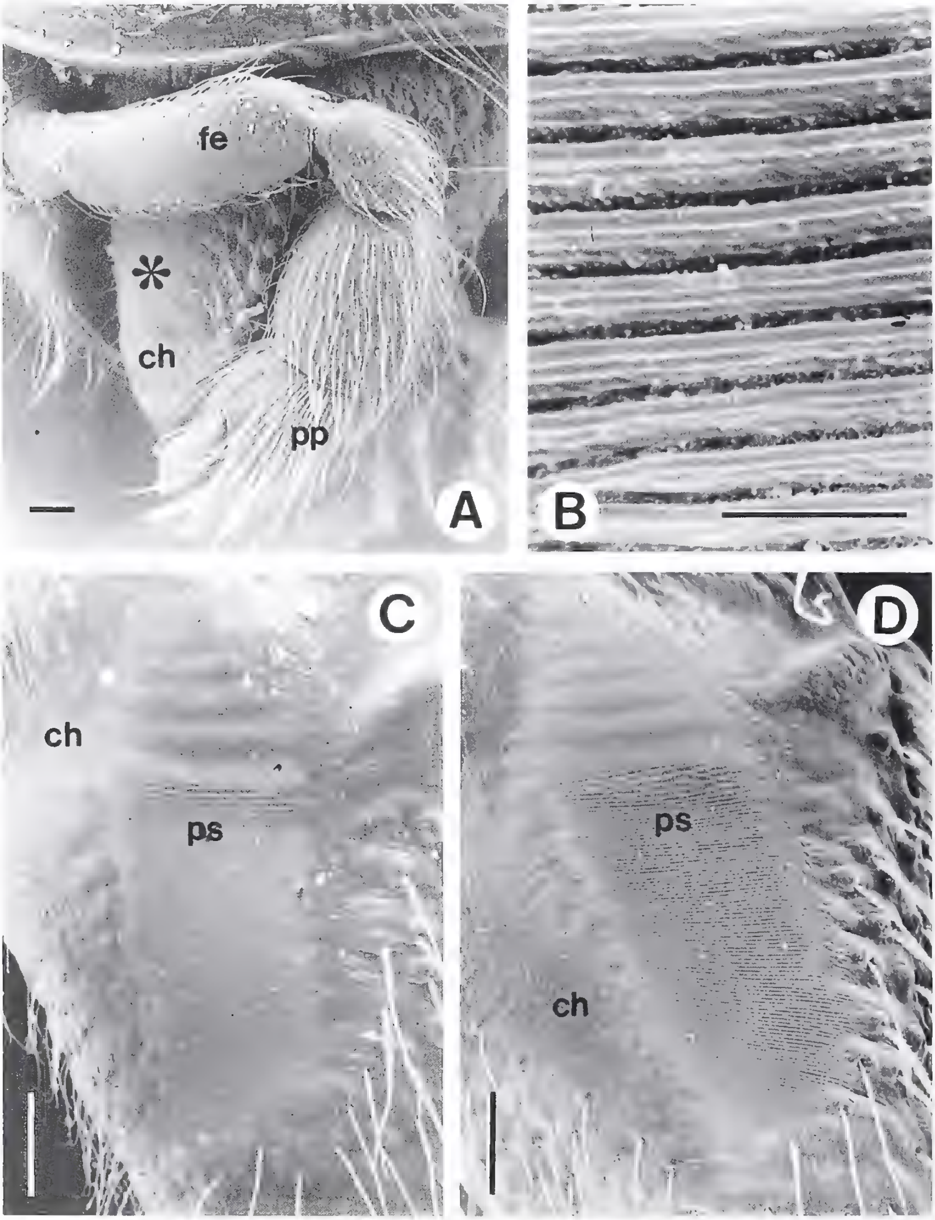

FIG. 1

A: Stridulatory apparatus of *P. gibbulus* (male from Sardinia), * position of stridulatory file. Scale line = 100 μm. B: stridulatory file, detail of the large ribs (female from Sardinia) Scale line = 10 μm. C: stridulatory file (male from Sardinia). Scale line = 100 μm. D: stridulatory file (female from Naxos). Scale line = 100 μm. ch: chelicerae; fe: femur; pp: pedipalpus; ps: pars stridens.

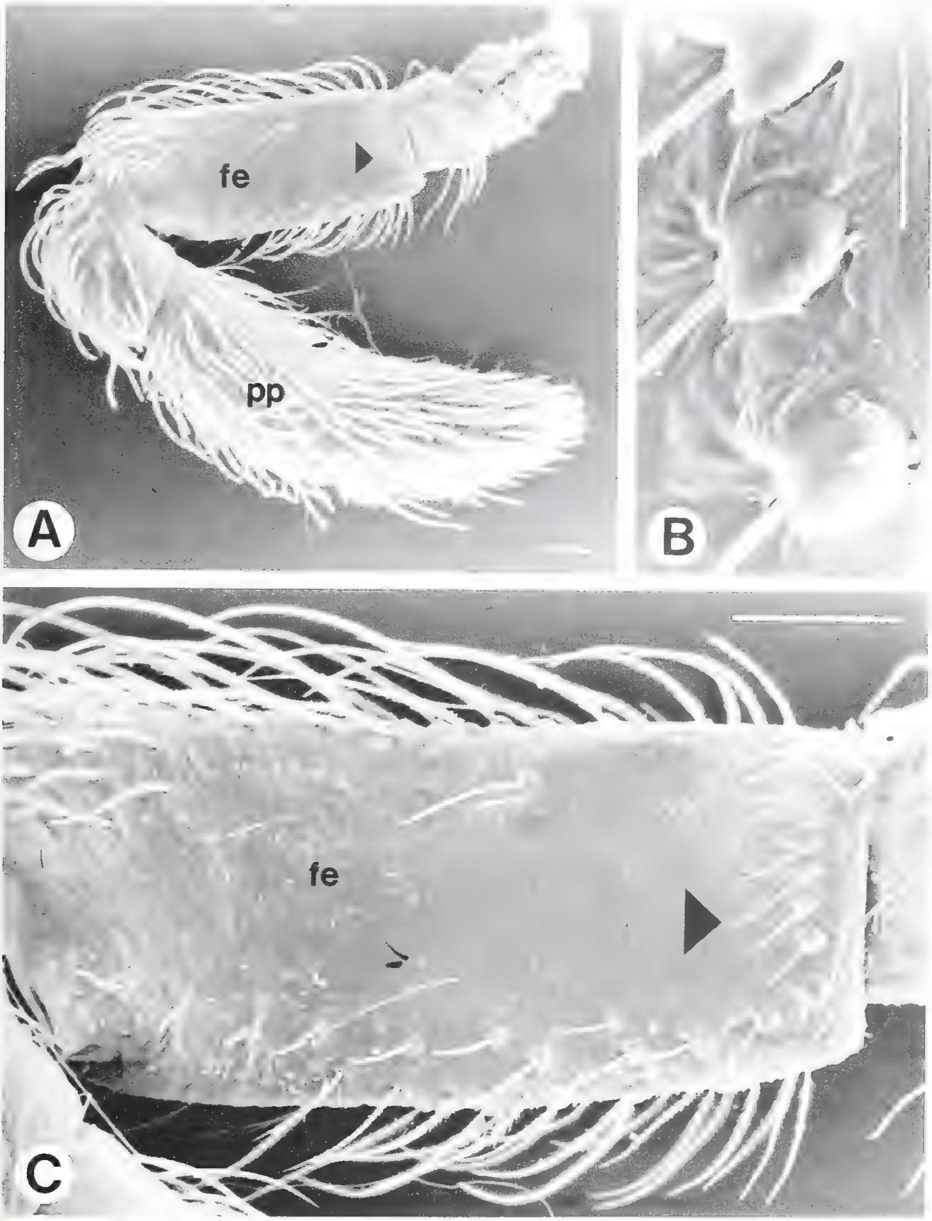

FIG. 2

A: Pedipalpus of *P. gibbulus* female from Sardinia, inner side. Arrow pointing towards plectrum. Scale line = 100 µm. B: Bristle bases on the plectrum. Scale line = 10 µm. C: Detail of the pedipalpal femur with row of bristles indicated by arrow. Scale line = 100 µm. fe: femur; pp: pedipalp.

Individual transferred to the laboratory stridulated as a reaction towards pinching, pushing or handling in general. Defence stridulation is usually accompanied by a threat position, whereby the large first pair of legs is raised. They possess a unique arrangement of spatulate hairs prolaterally on the tibia, metatarsus and tarsus (see figs. 279, 281 in FORSTER & PLATNICK 1984). In the following description of mating behaviour we refer to "stridulation" whenever the typical palpal movements occurred, although the sound is not audible from the distance necessary for undisturbed observation.

Mating was observed with 2 females and 1 male in 1992 and 1 female and 1 male in 1994. The females from 1992 did not allow copulation, although the male courted them. Courtship apparently commenced only after the first contact between the partners which appeared to occur by chance while the individuals moved about inside the box. After initial contact, females in both pairs stridulated. The male approached each of the females, touched them, retreated and stridulated from a distance of about 1 cm. The pair from 1994 engaged in a single copulation: after the male encountered the female face to face, he moved on to her prosoma, stridulated and quivered with his abdomen. The female moved slightly, lifted her first pair of legs and quivered with the second pair of legs. Whether the female stridulated as well could not be observed, as the mounted male concealed the view. The male moved onto the opisthosoma of the female who then quivered with increasing amplitude with her first and second pair of legs, stridulated briefly and lifted her body upwards into a

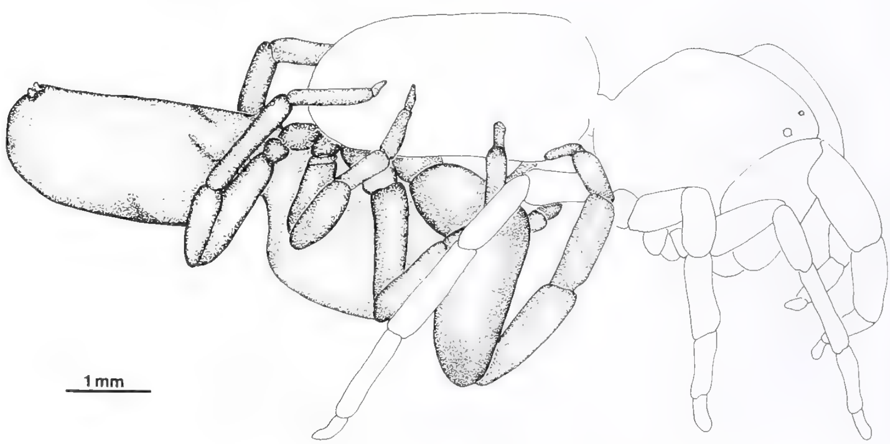

FIG. 3

Copulatory posture of *P. gibbulus*, drawn from a photograph taken by C. Gack. Female above, male below. Female pedipalps concealed by the large, first pair of legs. Male pedipalps are partially shown adjacent to the femur-patella joint of the female's fourth leg.

`tiptoe' position. Then the male turned to a parallel position and moved underneath the female who stayed in the tiptoe position. After a pause of about 40 s the male tapped the female with his second and third pair of legs while his large, first pair of legs served as a holdfast: the male's "knee" (femur-patella joint) was pressed against the ground whereas leg 4 of the female was clamped between his tibia and tarsus of leg 1 which are both well equipped with scopulae. The male's fourth pair of legs pressed against the caudal part of the female's opisthosoma. Copulation took place in this position (fig. 3). Before insertion, the male was observed to stridulate. Insertion of the palps took place in succession with the palps wriggling slightly during the first minute of insertion. After thirty-five minutes the female started to move, causing the male to jerk back and forth and then sideways with his entire body but without removing the inserted palp. The male again tapped the female with his second and third pair of legs and jerked. The female resumed movement, the male apparently withdrew the inserted palp and stridulated briefly. The female became increasingly active and carried the male still clinging to her around. 57 minutes after insertion the male loosened his hold, but remained close to the female in an antiparallel position and tapped her with his first pair of legs before separating.

Bioacoustics

Only stridulatory signals produced under artificial stimulation could be recorded. These signals show a simple and irregular temporal structure (figs. 4A, B) and a relatively homogeneous power spectrum (fig. 4C). Normally, the spiders produced a complex chirp caused by an upstroke and a downstroke of the pedipalp. We were not able to detect in which direction pedipalp movement started. The two strokes can be recognized in the chirps at ca. 10 ms, 45 ms and 70 ms. At ca. 55 ms a single up or downstroke was made and the corresponding down or upstroke was partly suppressed. Its traces can be seen at 60-65 ms.

The sonagram (fig. 4B) shows that the main frequency band (between 0.9 kHz and 1.4 kHz) of the signals was slightly tuned downwards from about 1.4 kHz to 1.1 kHz in the course of each chirp.

The power spectrum (fig. 4C) shows no frequency gap, only a shallow depression at ca. 1.8 kHz. Consequently, two power maxima can be identified: the first at 1.00 kHz, the second at 2.42 kHz. The upper end of the frequency range is ca. 8 kHz.

DISCUSSION

The chelicera-pedipalp stridulatory apparatus of *Palpimanus gibbulus* is classified as type d according to LEGENDRE (1963). Following this classification, the apparatus of *P. gibbulus* belongs to type dII, named "organe de Simon" after SIMON, who first described this organ type in the genus *Sicarius* in 1893. According to a later classification by STARCK (1985), the apparatus of *P. gibbulus* would be classified as a type d1 organ. The morphology of the stridulatory apparatus of *P. gibbulus* is very

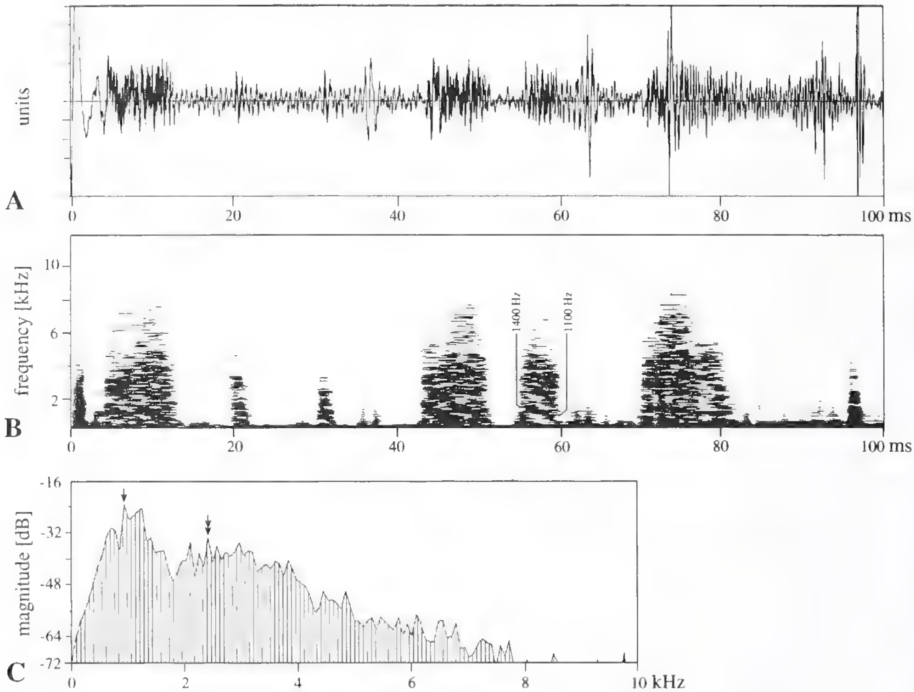

FIG. 4

A: Oscillogram, B: sonagram and C: power spectrum of stridulatory sound of a *P. gibbulus* female from Sardinia. In A and B the chirps at ca. 10, 45 and 75 ms represent sounds produced by an up and downstroke of the pedipalp, while the chirp at ca. 55 ms was caused by an isolated up or downstroke. In B, the slightly tuned main frequency band is marked for the chirp at ca. 55 ms. The vertical axis in C is scaled in relative units. No attempt was made to calibrate the sound energy measurement. The arrow points to the first power maximum at 1.00 kHz, the double arrow to the second at 2.42 kHz.

similar to the apparatus described for *P. stridulans* by LAWRENCE in 1963. A yet unpublished SEM studies by N. Platnick (pers. comm. 1995) demonstrate that at least three American palpimanid species (*Anisaedus stridulans* González, *Anisaedus pellucidae* Platnick, *Otiothops lanus* Platnick) also have cheliceral stridulatory ridges. The chelicera-pedipalp stridulatory apparatus seems to be the prevalant mode of sound production in Palpimanidae.

In *P. gibbulus*, stridulation is employed in at least two different behavioural contexts: defence and intersexual communication. Juveniles and adults of both sexes engage in sound production when attacked or otherwise disturbed, whereas only males unequivocally stridulate during courtship and copulation. With regard to females, the situation is not as clear: both females that did not mate exhibited stridulation on the first encounter with a male. This could have been a defence reaction as

well as intersexual communication. In the pair that engaged in mating, the female stridulated briefly during courtship however significantly less than the male. Since only one complete mating could be observed, it remains unclear whether the observed difference represents the typical mating behaviour of *P. gibbulus*. Whether stridulation is used in the context of male-male aggression as in the Theridiid spider *Steatoda bipunctata* (GWINNER-HANKE 1970) also remains an open question, because no more than one male was available at a time. Unfortunately, Palpimanids occur at low population densities, thus making a more detailed investigation difficult.

Bioacoustics

The simple and irregular temporal structure of the stridulatory signals as well as the lack of any marked frequency gap indicate that these chirps are disturbance signals (cf. MASTERS 1980). Typical intraspecific stridulatory signals are highly regular, possess a complex temporal pattern (BAILEY 1991:104, grasshopper songs) and show marked frequency gaps (RIEDE & KROKER 1995, cicada songs). However, we cannot exclude the possibility that *P. gibbulus* produces different sounds in the context of intraspecific communication, e.g. by a different movement pattern of the pedipalp or by scraping over another part of the file, e.g. the proximal portion only (fig. 1).

The sonagrams look similar to those from sounds produced by a double stroke of a file-and-scraper organ, e.g. in the longicorn beetle *Dorcadion fuliginator* (SCHMITT & TRAUE 1990). The slightly downward tuning of the main frequency band is probably without a biological meaning since each single stroke in a backwards-and-forwards movement has to slow down at the turning point, which inevitably leads to a frequency modulation that is observed regularly in stridulatory sounds, e.g. in criocerine leaf beetles (SCHMITT & TRAUE 1990).

Probably only the vibrational component of the sound acts as a defence against possible predators or parasitoids because the power maxima are at relatively low frequencies (1.00 kHz and 2.42 kHz). In this frequency range sound is best propagated through substrate vibration (see MARKL 1968, MASTERS *et al.* 1983). The emitted sound energy was not measured but must be very low since the sounds are nearly inaudible to the human ear.

The bioacoustic analysis refers only to female spiders. Male signals have not been analysed. Although there are no distinct morphological differences in the stridulatory apparatus of both sexes, differences in the resulting signal are still possible. Moving the plectrum more or less quickly across the file or across the two areas that show differences in rib size may lead to a distinctively different signal. We cannot deduce from the analysis of the defence sounds that the signal produced in intersexual (or intrasexual) contexts has similar characteristics. If *P. gibbulus* produces similar sounds during courtship and copulation then the mating partners could also use the vibrational components as signals and perceive them by means of the lyriform organs. However, the two mating individuals were observed to stridulate only when they were at a distance of less than 2 cm (if not in physical contact). This distance lies within the near field (radius < 1/6 of the wavelength). The animals can thus probably perceive

the sound velocity of the airborne component by means of their trichobothria. This mode of sound perception is often suggested for spiders but no reliable evidence has been reported (MARKL 1969; BARTH 1982).

Our findings concerning courtship display and mating position of *P. gibbulus* differ from GERHARDT's description (1927) in various aspects: he does not mention the courtship behaviour of the female and states that it is the male who ends copulation whereas we found that the female engages in courtship and may end copulation. Additionally, GERHARDT does not refer to any movements of the pedipalps that might be related to stridulation. Also, his description and drawing of the mating position differ somewhat from what we observed and he does not mention the locking mechanism of the male on the female during copulation in which the male's first pair of legs holds the female's fourth pair of legs.

In conclusion, the Palpimanidae are added to the list of 22 families of spiders in which stridulation is known to occur for at least some members of each family (UETZ & STRATTON 1982). The same applies to some other spider groups. Based on recent literature and some not previously cited, the following 8 families are added: Amaurobiidae (DAVIES 1986), Archaeidae (Millot 1948 in LEGENDRE 1970, FORSTER & PLATNICK 1984), Austrochilidae (FORSTER *et al.* 1987), Caponiidae (BRIGNOLI 1977, PLATNICK 1993, 1994*a*,*b*), Gradungulidae (FORSTER *et al.* 1987, DAVIES 1993), Mecysmaucheniidae (FORSTER & PLATNICK 1984), Pararchaeidae (FORSTER & PLATNICK 1984) and Stenochilidae (PLATNICK & SHADAB 1974), bringing the total to 31 families of stridulating spiders.

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Modelling individual variability in a social spider colony (*Stegodyphus dumicola:* Eresidae) in relation to food abundance and its allocation

Karin ULBRICH[1], Johannes R. HENSCHEL[2], Florian JELTSCH[1] & Christian WISSEL[1]

Modelling individual variability in a social spider colony (*Stegodyphus dumicola:* Eresidae) in relation to food abundance and its allocation. - An individual-oriented model is developed to describe the population dynamics of social spiders. As a consequence of group living, individuals affect each other's behaviour, development and reproduction. As an example, the spider *Stegodyphus dumicola* (Eresidae) is investigated. The survival and development of individual spiders and of the colony depends considerably on food availability. The model demonstrates that complex behavioural functions, such as competition over food, can lead to distinct individual variances in body-masses of spiders at all life stages. The model results confirm field observations about the association between contest competition and individual variability. Colonies in which individual variability in body-masses was high due to contest competition survived longer in periods of food scarcity than colonies with scramble competition where the variability was lower.

Key-words: individual-oriented model - social spiders - contest competition - scramble competition - individual variability - colony survival - *Stegodyphus*.

INTRODUCTION

Non-territorial permanently social spiders share their food and may compete for this resource (Ward & Enders 1985; Vollrath 1986; Rypstra 1993; Willey & Jackson 1993). A dominance hierarchy in the group can lead to unequal sharing, with some spiders receiving more than others (Rypstra 1993). Alternatively, food may tend to be evenly or randomly distributed among group members. This could be the case with small prey that individual spiders appropriate for themselves, or with solitary-living conspecifics.

[1] UFZ-Centre for Environmental Research Leipzig-Halle Ltd., Permoserstr. 15, D-04318 Leipzig, Germany.

[2] Desert Ecological Research Unit of Namibia, P.O.Box 1592, Swakopmund, Namibia.

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Members of social groups of *Stegodyphus dumicola* Pocock, 1898 (Eresidae) in Namibia differ considerably in size (HENSCHEL *et al.* 1995). From this variation, which occurs within the same cohort and sex, one can deduce that individuals differ in development rate. Ultimately, such differences should be reflected in variable reproductive success (SEIBT & WICKLER 1988; HENSCHEL *et al.* 1995; see also RYPSTRA 1993). This variability is probably a consequence of competition among group members over food.

We focus on two questions: (1) how does the degree of competition for food affect colony development and (2) how does variance in individual fitness affect the survival of colonies. We developed an individual-oriented model which allows the investigation by simulation of colonies over many generations under specified conditions. We base the model on life-history parameters reported for different *Stegodyphus* species (SEIBT &WICKLER 1988; SCHNEIDER 1992; WARD & LUBIN 1993) with emphasis on *S. dumicola* in Namibia (HENSCHEL *et al.* 1995; HENSCHEL 1996).

In order to investigate the influence of competition over food on colony development, we use two contrasting scenarios based on rules of two extreme types of intraspecific competition – "contest" and "scramble" (NICHOLSON 1954). Contest competition, in which dominant individuals feed before others, leads to a predictable and biased allocation of resources. A stable, linear social hierarchy is an extreme of this case (e.g., HENSCHEL & TILSON 1988). By contrast, food allocation is unpredictable in scramble competition where any individual can obtain much food from captured prey at one occasion and little on another occasion. This may depend on the time of arrival of an individual at prey, the availability and quality of vacant positions at prey that it can occupy, and other (stochastic) factors. Individuals in scramble competition do not displace each other, but compete by feeding, thus reducing the amount left for others.

The current report concerns the first step of a model being developed to examine factors involved in the evolution and maintenance of sociality in spiders. For the present, we focus on the influence of food allocation and leave aside other possible factors, such as predation risk, emigration and interactions between colonies, that may affect the development of a particular colony. We limited the growth and longevity of a colony only by food resources and concentrate on the relative differences caused by contest and scramble competition. This allows us to make a preliminary, qualitative assessment of the role of food availability and competition in spider sociality.

METHODS

Phenology and development

Stegodyphus dumicola is a 100–260 mg spider (adult female size) that occurs in colonies comprising a few to hundreds of individuals (SEIBT & WICKLER 1988), or it occurs solitarily when a female disperses alone (HENSCHEL 1993, 1996). Colony members share common retreats and build large capture webs to trap flying or

jumping insects. Captured prey includes small insects that one individual can consume alone as well as large insects that are shared. *Stegodyphus dumicola* has an annual life cycle with non-overlapping generations, except during the nursery period (Fig. 1). The overall secondary sex-ratio is female-biased (female proportion = 88%). As a consequence of variance in growth, females mature more asynchronously and often later than the males (Fig. 2; HENSCHEL *et al.* 1995). Adult males are short-lived and females that mature too late may have no opportunity to mate. HENSCHEL *et al.* (1995) suggested that the relative timing of reproduction by different females in a colony may determine the size and development rate of their offspring.

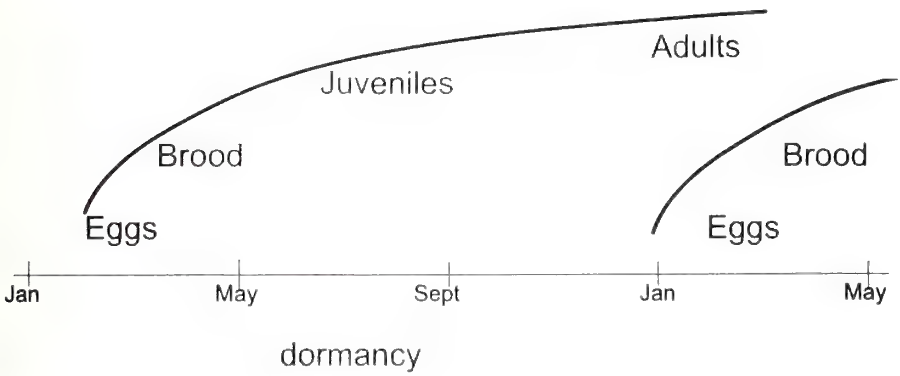

FIG. 1

Life cycle of *Stegodyphus dumicola* in Namibia, after HENSCHEL (1996). The first eggs are deposited in February; the brood hatches after two weeks; the nursery period precedes a dormancy period during June to August; the first adults mature in January.

The model-assumptions and rules

Parameters for the model are derived from field data (op. cit.) and are applied to the life cycle of the individuals within one colony. The time step is one day, as processes such as food allocation and reproduction have a resolution at this time scale. We distinguish between the main life stages: egg, brood, juvenile and adult. Rules for foraging, growth and reproduction are given for each of these stages. Indices are developed for individuals ($_i$) and colonies ($_c$). The parameters and their ranges are listed in Table 1. The values for parameters f1–f7 were varied systematically in a limited range or had fixed values; their role was to yield realistic ranges of values for the dependent parameters in each equation.

FORAGING – We assume that spiders can eat every day. As larger colonies have larger capture webs (Henschel, unpubl.data), the daily food resource ("food$_c$") for the colony has a linear relationship with colony size as follows (eq. 1):

$$food_c = f1 * (f2 + f3 * (size + drand)) \qquad \textbf{(1)}$$

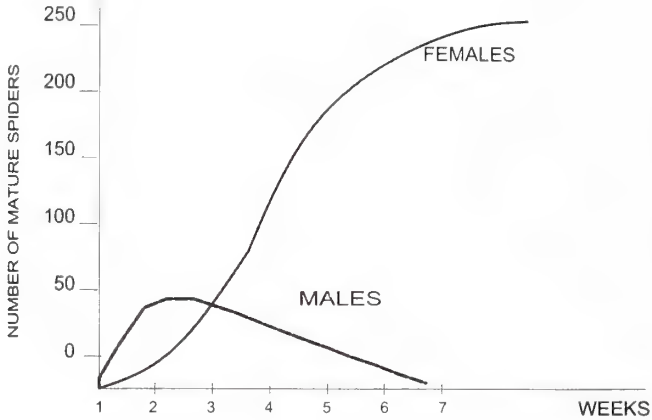

FIG. 2

Early maturation of males followed by asynchronous maturation of females of *Stegodyphus dumicola* (redrawn after HENSCHEL *et al.* 1995).

TABLE I

Model parameters

Parameter	Definition	Range	Dimension
f1	food level	1–6	
f2	parameter (eq. 1)	5	
f3	"	0.75	
size	colony size	0–700	
eat	daily food uptake	0–6.3	mg
need	daily need	0.75–6.3	mg
f4	parameter (eq. 4)	0.75–5.5	
f5	"	10–100	
f6	parameter (eq. 10)	0.5	
f7	parameter (eq. 10)	0.5	
resource	food resource		
energy metabolism		0.1–1.3	mg
eggnumber	size of clutch	10–100	

The parameter f1 represents the "food level", which is varied between different simulations. A food level of 1 is in accordance with a daily food availability in a range of 0.8 mg to 1.55 mg per spider. This is valid if the colony size is 100 and f2 = 5 and f3 = 0.75. Parameter f2 is the minimum amount of food, which is available for the colony independent of its size. The colony size is the number of juveniles and adults. Parameter f3 refers to the effect of the colony size on the daily food resource

$food_c$. The daily stochasticity of this relationship is expressed by means of the random function "drand", returning values from 0 to 1.

The food uptake ("eat_i") by an individual spider (i) is determined by the amount of food required ("$need_i$"), limited by the amount available at the time this individual feeds ("$resource_i$"). The individual takes the amount of food it needs or, if the resource available to the individual is smaller than the amount needed, it takes this resource (eq. 2):

$$eat_i = minimum(resource_i, need_i) \quad \textbf{(2)}$$

The food obtained by an individual depends on the type of food allocation, based on two rules of competition. The first is "contest" or hierarchical competition, with larger spiders having priority of access to food and receiving more food than small ones (RYPSTRA 1993; M. Whitehouse, pers. comm.). In this case, the individual resource for the largest spider ("$resource_i$") is the daily food resource ("$food_c$", see eq. 1). In the corresponding model procedure, the dominant (largest) individual has first choice of food, followed by others successively down the body-mass hierarchy until no food is left. In this way, the resource available to spider (i) depends on the food consumed by the spider that preceded it (eq. 3):

$$resource_i = resource_{i-1} - eat_{i-1} \quad \textbf{(3)}$$

The need of a spider depends on its body-mass ("$mass_i$") (ANDERSON 1970). Since little is known about the actual relationship for *S. dumicola*, we approximate this with eq. 4:

$$need_i = f4 + \frac{mass_i}{f5} * drand \quad \textbf{(4)}$$

Parameter f4 is the part of the individual need which is independent of the body-mass. The second part depends on the body-mass ("$mass_i$") and is varied by the random function "drand". For comparison with "contest" competition, we consider also "scramble" competition, in which the succession of access by individuals to food is changed randomly each day. Over long time periods, this random allocation of food tends to lead to an even distribution of food among colony members.

GROWTH – The growth of spiders is described by their change in mass ("Δ $mass_i$"), which is the result of feeding minus the energy required for metabolism and activities:

$$\Delta mass_i = eat_i - energy_i \quad \textbf{(5)}$$

An individual died of starvation if its mass declined to <50% of a mass that it had attained previously.

REPRODUCTION – Rules for reproduction depend on maturation, fertilization and egg laying. Due to the different maturation rates of males and females (Fig. 2) the operational sex ratio at the beginning of the mating period can be male-biased

(HENSCHEL *et al.* 1995). Therefore, the probability of reaching maturity in the first week of January is assumed to be higher for a male than for a female (eq. 6, 7). The actual date is described by the parameter "day".

$$p_{maturity_{male}}(day \leq 7) = \frac{day}{7} \tag{6}$$

$$p_{maturity_{female}}(day \leq 7) = 0{,}001 \tag{7}$$

Model females only mature at a mass >120 mg. After the first week, the probability of maturation per day increases for females:

$$p_{maturity_{female}}(day > 7) = 0{,}1 \tag{8}$$

All model males mature during the second week of January. All model females that mature in the first 14 days are fertilized. As males are available for reproduction only for a short period of several weeks (HENSCHEL *et al.* 1995), a rule for male mortality is introduced after the second week of January:

$$p_{mortality_{male}}(day > 14) = 0{,}1 \tag{9}$$

Due to the decreasing number of males, a further model rule expresses the fertilization of only the biggest virgin female every day after the first two weeks until all males disappear. The mortality of females increases after the beginning of April, as females are consumed by juveniles during this period.

Following the trend that larger spider females have a higher fecundity (SCHNEIDER 1992), our model spiders produced eggs according to their body-mass:

$$eggnumber_i = f6 * Weight_i^{f7} \tag{10}$$

Simulation runs

Colonies arbitrarily comprised 100 members upon entering the simulations. The development of individuals and colonies was tracked on a daily basis and an annual basis respectively. Records of the mass of individuals and of colony size were taken on 31 December, immediately prior to the first maturation. A colony goes extinct when none of the females is capable of reproducing. The time span to this condition is referred to as "colony life time". Mean colony life time for a certain food level was calculated over 100 simulations.

RESULTS

Contest competition over food leads to considerable individual variation in the development of different life stages (Fig. 3; CV = 22.5%). By contrast, scramble competition yielded significantly lower variances in mass (CV = 6.6%; $F_{151,218}$= 37.8, P < 0.001). Under conditions of food scarcity, none of the spiders reached maturity in colonies with scramble competition while some still succeeded in colonies with contest competition.

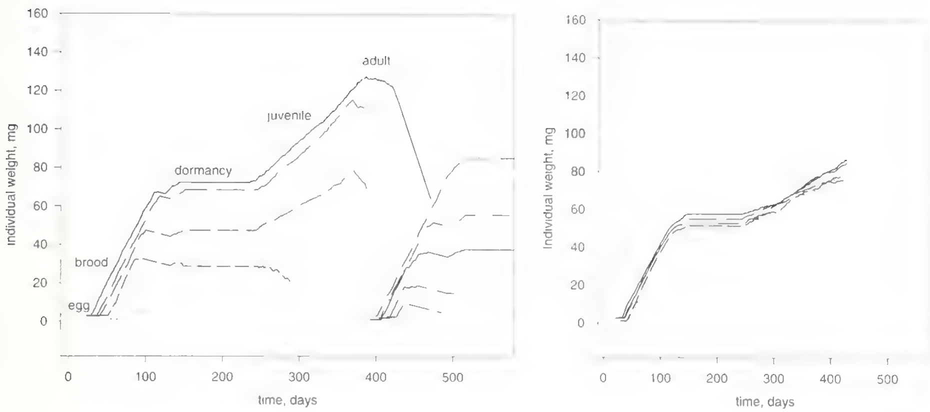

FIG. 3

Individual mass change over time of five randomly selected individuals in two successive generations in (a: left) a colony with contest competition and (b: right) a colony with scramble competition. The colony with scramble competition was extinct after one generation because no females reached maturity. The food level was 1.

Contest competition led to distinctively longer colony life times than did scramble competition (Fig. 4). Under conditions of food scarcity reproduction is possible only in a hierarchical colony with contest competition. In both conditions, mean colony life time correlated closely with the food level ($r_2 = 0.97$ and 0.93 for contest and scramble competition respectively, $P < 0.001$; log(y) - transformation). Therefore, mean colony life time increases exponentially with increasing food level. The slopes of the regression equations differed significantly ($t = 4.46$, $df = 15$, $P < 0.001$; test follows ZAR 1984), being steeper for contest competition. Even slight increases of the values of food level (fl in eq. 1) caused considerable increases in the life time of colonies with contest competition. By contrast, colonies with scramble competition required higher food levels for reproduction to occur within them. Large increases in food level were necessary to cause slight increases in the average colony life time.

How colony development is affected by food abundance was demonstrated by tracking colony size over successive years under relatively different food conditions in colonies with contest competition (Fig. 5). At low food levels, the colony size varied in the range between 15 to 150 members. A threshold in colony growth was evident when the food level increased from fl = 4 to fl = 5. Above this threshold, the probability of colony extinction is low. Since there is ample food, few if any spiders die of starvation. With many adults of both sexes present, demographic stochasticity is low.

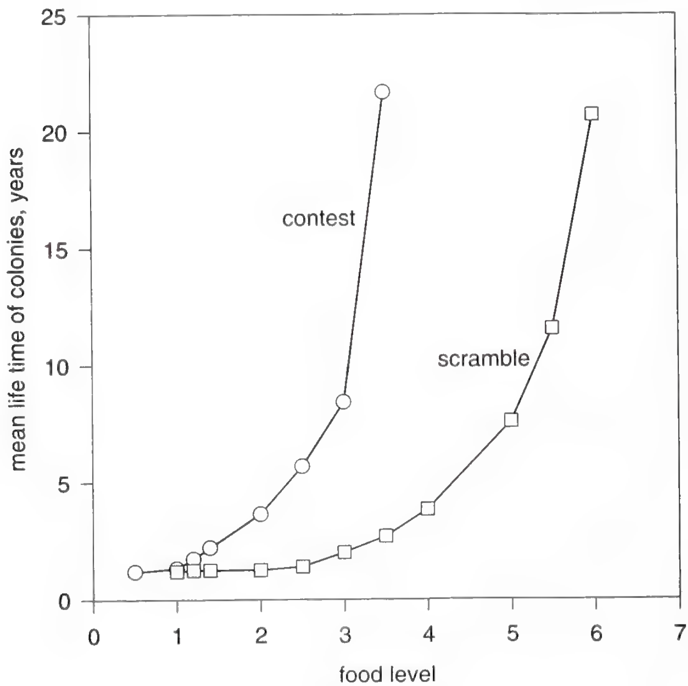

FIG. 4

Mean colony life time in over 100 simulations each of colonies with contest and scramble competition under various levels of food richness (f1 variable in eq. 1).

DISCUSSION

The calculations incorporated into our model are very sensitive to the mathematical description of food availability and its allocation. Nevertheless, such modelling yields qualitative results that can point out the direction of the next step to be taken. In this initial approach, we have neglected limiting factors other than food shortage; therefore our model colonies could attain unrealistic sizes of up to thousands of spiders, whereas in reality S. dumicola colonies contain, at most, hundreds of individuals. Through our approach, it is possible to highlight the qualitative differences resulting from different food-sharing strategies.

Our model demonstrates that the unequal distribution of limited food among members of social groups appears to have a considerable effect on colony survival. In colonies with contest competition, juveniles that hatched early in the season maintained a life-long size advantage over juveniles that hatched later. Nevertheless, small spiders also took part in nest and web maintenance, and the overall food resources increased as a result of their work (see eq. 1). Thus, large spiders increase their

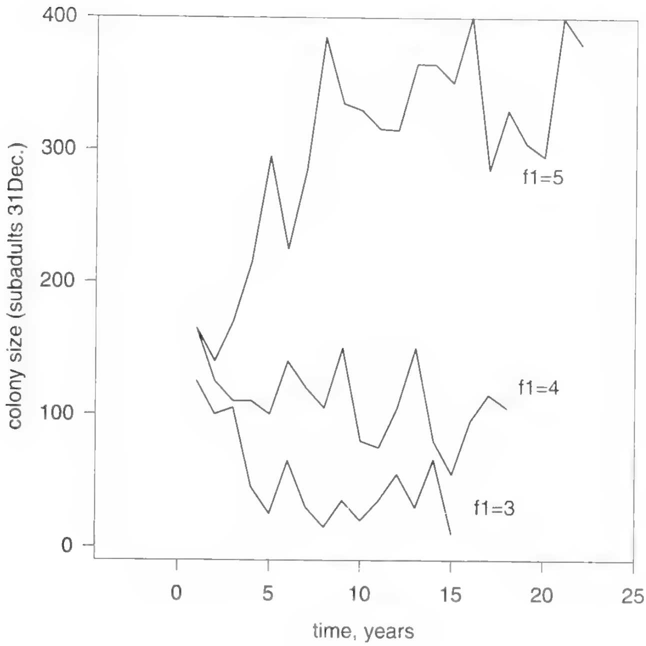

FIG. 5

Colony size development over years of colonies with contest competition at various levels of food richness. Colony size was calculated as the number of spiders present on 31 Dec., shortly before first maturation.

resource gain and, ultimately, the probability of survival, at the expense of the small spiders. The model calculations are consistent with observations that have suggested that individual variation is associated with contest competition (VOLLRATH 1986; RYPSTRA 1993; HENSCHEL *et al.* 1995).

Contest competition leads to high variance in individual development rates within colonies, which has a stabilizing effect on the colony size and thereby prolongs the survival of the colony. In other words, the maintenance of a feeding hierarchy lowers the risk of colony extinction. We explain this in terms of the different allocation of limited resources. In colonies with contest competition, at least some dominant females are likely to reach the threshold size for reproduction (RYPSTRA 1993), except when food is extremely scarce. In colonies with scramble competition, however, even moderately high food supply may not suffice to get any of the similarly-sized females above the reproductive threshold in time to mate.

According to the results of our model, colonies with contest competition tend to grow consistently (with some fluctuations) at a high level of food richness (Fig. 5). A food coefficient of 5, which lies just above this growth threshold, is an average daily food availability of 4.0 to 7.75 mg per spider in a colony of 100 individuals.

Above this growth threshold, colonies are not expected to go extinct if there are no negative factors other than starvation and failure to reproduce.

We conclude that high variability among individuals reduces variability in colony size in successive generations and enhances colony survival when food richness is below a critical level. We intend to incorporate this conclusion into the next step of the model. This is to examine the effect of environmental stochasticity that causes within- and between-year variability in food availability. This should not only broaden our understanding of how food parameters affect colony size and survival, but also how they affect the fitness of individuals in the colony compared to that of solitary dispersers.

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Spatial distribution and dispersal of spiders in a Danish barley field

Claus VANGSGAARD
Dept. of Zoology, University of Aarhus, Universitetsparken,
DK-8000 Aarhus C, Denmark.

Spatial distribution and dispersal of spiders in a Danish barley field. - Spiders were collected in pitfall traps in a transect running from a forest, through an unmanaged grass strip, into a field with spring sown barley. Plastic buckets were used to monitor ballooning activity. Numbers of species and specimens caught along the transect are described. Spatial distributions of the predominant species are illustrated. Dispersal patterns of these lycosid and linyphiid spiders are analysed and the importance of nearby habitats is discussed. It is concluded that the life cycles of the lycosids depended on the forest and the grass strip. However, the life cycles of the predominant linyphiids are not directly dependent on the nearby habitats.

INTRODUCTION

During the recent twenty years increasing interest has been paid to the importance of field edges and other nearby habitats for the dynamics of polyphagous predators in agricultural systems. The importance of polyphagous predators as control agents of pests in agricultural systems has been demonstrated by many authors (POTTS & VICKERMANN 1974, EDWARDS *et al.* 1979, RIECHERT & LOCKLEY 1984). Impact of spiders on pest species in different crops have been analysed in a number of papers (See NYFFELER & BENZ 1987 for a review). And migration from field edges are studied in a number of papers on beetle migration (eg. DUELLI 1990, BLICK & BLISS 1991, LAGERLÖF & WALLIN 1993). However, only a few studies contributes to the knowledge of field edges as a potential reservoir for spiders (BISHOP 1981, VANGSGAARD *et al.* 1990, BAYRAM & LUFF 1993). Spider migration studies have mainly focused on ballooning activity (VAN WINGERDEN & VUGTS 1974, MEIJER 1977, DUFFEY 1956,1978, GREENSTONE 1982, DEAN & STERLING 1985, AGNEW & SMITH 1989). However, the problems of interpreting ballooning data are considerable - eg. are the numbers net migration or is it just exchanges between different fields? Another problem concerns the fate of the individual spider. Did it only fly 10 metres or did it come from a distant habitat. Or was it just a mistake landing on the study area, so that it would have taken off if not collected by the scientist?

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As long as a practical methodology for interpreting ballooning data has not been worked out it seems that the only way of studying spider dispersal is to compare distribution patterns during spring and summer in transects running from field edges to field centres. This approach could reject the hypothesis of nearby habitats functioning as reservoirs or wintering areas of spiders. Topping & Sunderland 1995 described a method to interpret ballooning data, but further studies should confirm the applicability of their technical solution. The aim of this paper is to discuss effects of the field edges on the species composition in the field and to discuss movement patterns in different species. And further to discuss the very important question - do field edges help the spider community in controlling pest species?

STUDY AREA AND METHODS

The study was carried out on a field near Rønde, Jutland (56.17N,10.28E) belonging to the Danish Environmental Agency (DEA). The field "Stegelykke" was mainly used for studies on short and long term effects of pesticide spraying. The field was bordered to the west by the "Hestehave" forest (beech), a saltmarsh to the south, and east and north by other fields. Northern and southern field edges consisted of small gravel roads, whereas the eastern field edge was a main road edged with a hedge of old trees and shrubs. The spider fauna of the forest is known from a two year study by Toft (1976). The study plot ran from 3 metres inside the Hestehave forest to the centre of the field. The vegetation of the field edge consisted of a mixture of different tree species outside the beech forest and a rich herbage layer. The unsprayed barley was sown on the 1. April and harvested on the 16. August. Spiders were collected in pitfall traps in a transect running from a forest, through a 2 metre broad unmanaged grass strip, into a field with spring sown barley. Seven rows of five pitfall traps were placed with rows at 3 metres into the forest, at the grass strip 1 metre from the field edge, and at a distance of 1, 5, 25, 50, and 75 metres into the field. The distance between traps in a row was 2 metre. The pitfall traps were made of plastic and had a diameter of 65 mm and were 10 cm deep. Each trap were half-filled with a saturated water solution of benzoic acid and a detergent. Ballooning activity was monitored by means of 3 plastic buckets and the same trapping fluid. These buckets were placed on the ground 25, 50, and 75 metres inside the field. The vegetation around the buckets where removed to prevent spiders dropping from the crop into the buckets. The traps were sampled every week from the 5. March to harvest on the 12. of August.

Spiders were identified using Locket & Millidge (1953), Roberts (1985, 1987), and Heimer & Nentwig (1991). All adult spiders were identified to species and juveniles to family or genus level. The nomenclature used was that of Merrett *et al.* (1983). However, a small numbers of species not included in the British fauna were named following Heimer & Nentwig (1991).

Differences between rows were studied by means of an index of similarity: S=2c/a+b, where c is the number of species common to both rows and a and b are the

total number of species in each row. Relative "mean position" from field edge of important species was computed from the expression

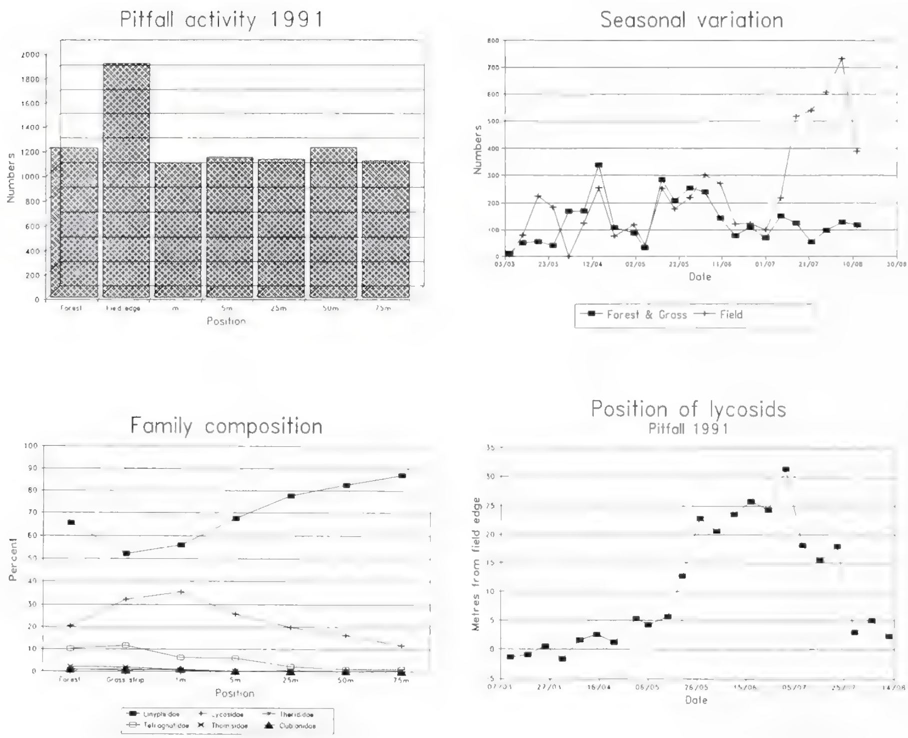
$$P = \frac{\sum}{N_{tot}} (P_i * N_i)$$

where Ni is the number of individuals in trap row i, Pi is the distance from the field edge, and Ntot is the total number of individuals of that species (VANGSGAARD *et al.* 1990). These "mean positions" were computed for each trapping period and as an average for the trapping season. Principal Component Analysis were used for indirect ordination. The software used was CANOCO (BRAAK 1988) for ordination and CANODRAW for graphical output (SMILAUER 1990).

RESULTS

A total of 8709 specimens of 124 species were collected in 1991. The 124 spider species represented 15 families. Juveniles, that were identified to family or if possible to genus, accounted for about 15% of the total numbers. Ballooning activity was low in 1991, where only 120 specimens of 20 species were caught. B.gracilis, which is the dominant spider in the highest part of the barley crop, accounted for 40% of the spiders caught. The pitfall trap catches of spiders was evenly distributed over the transect except activity was higher in the grass strip (fig.1). However, the activity in the field increased during the growing season whereas activity declined in the forest and at the grass strip (fig.2). Numbers of species declined from the field edge to the centre of the field. Further, there was a shift in dominance between different families from the forest to the field centre (fig.3). The relative numbers of linyphiids were 65% in the forest, 52% at the grass strip, and it rose to 87% in the centre of the field. This increase in linyphiid numbers was followed by a corresponding decrease in wolf spiders. The Tetragnathidae (only *Pachygnatha* species) were important in the forest and at the grass strip, but the relative numbers declined from about 10% to 5% at the 1 and 5 metre rows and further down to about 2% in the centre of the field. The relative abundance of linyphiids increased during summer from 51% in mid-april to more than 80% in August due to the dominant species such as *E.atra* and *Oe.apicatus*. The relative abundance of lycosids rose from about 10% in April to more than 40% in mid June.

The dominant species were *Pachygnatha listeri* Sundevall,1830, *Diplocephalus picinus* (Blackwall,1841), *D.latifrons* (O.P.-Cambridge,1863) in the forest. *Pardosa lugubris* (Walckenaer,1802), *Pachygnatha listeri*, *Pelecopsis radicicola* (L. Koch,1872), *D.latifrons* and *D.picinus* dominated in the grass strip. *Bathyphantes gracilis* (Blackwall,1841) and *Pardosa lugubris* dominated in the field margin (1 metre and 5metre rows), and *Erigone atra* Blackwall,1883, *Meioneta rurestris* (C.L. Koch,1836), and *Oedothorax apicatus* (Blackwall,1850) in the centre of the field. However, two species - *E.atra* and *Oe.apicatus* - accounted for more than one-third of the total numbers caught.



FIGS 1-4

Fig. 1: Pitfall activity 1991; Number of individuals caught in the different pitfalls from March to August; Fig. 2: Seasonal variation in spider numbers caught inside versus outside the field; Fig. 3: Family composition; relative numbers of the most important spider families caught in the different pitfall rows; Fig. 4: Position of lycosids; wolf spider dispersal into the field. The represented points are the mean position of all wolf spiders.

The position of lycosids (fig.4) shows a shift from the forest edge to the centre of the field from May to June. This was especially evident in *Pardosa prativaga* (L. Koch,1870), and, to a lesser extent, *Trochosa ruricola* (Degeer, 1778) and *P.lugubris*. The dominant linyphiids showed no seasonal dispersal patterns. Table 2 shows the average position of the populations of some important linyphiids and lycosids. A position value higher than 22.3 means that the population are less numerous near the field edge, and contrary, a value smaller than 22.3 means that the species are more numerous near the edge. The two *Oedothorax* species have the highest values, but also the *Erigone* species and *Meioneta rurestris* have values above 30. *Bathyphantes gracilis* have an evenly distribution over the field. *Lepthyphantes tenuis* (Blackwall, 1852) tends to be more numerous near the field edge (a value of 10.6).

TABLE 1

Similarity between the rows of the transect.

	Forest	Grass	1metre	5metre	25metre	50metre	75metre
Forest	-	0,77	0,71	0,54	0,39	0,41	0,37
Grass	0,77	-	0,61	0,59	0,43	0,41	0,36
1metre	0,71	0,61	-	0,75	0,59	0,58	0,51
5metre	0,54	0,59	0,75	-	0,67	0,64	0,51
25metre	0,39	0,43	0,59	0,67	-	0,76	0,59
50metre	0,41	0,41	0,58	0,64	0,76	-	0,67
75metre	0,37	0,36	0,51	0,51	0,59	0,67	-

As supposed similarity between rows declined with increased distance (Table 1). There was a high similarity between the forest and the grass strip and between the field rows. However, there was a tendency towards an edge zone with similarities between the 1metre and 5metre rows higher than between the 5metre and 25metre rows. Principal Component Analysis revealed a clear grouping of spiders (fig.5). The typical agricultural spiders such as *Pardosa prativaga*, *Erigone atra*, *Oedothorax apicatus* and *Meioneta rurestris* are placed close together in the 2. square. The spiders from the grass stripe were represented in the first square and the spiders from within the forest in the fourth square. The PCA-plot of sites (fig.5) follows closely the results from the species plot. The forest site is in the 4. square, the edge site in the 1. square and the remaining sites are placed in a row from the 2. to the 3. square. The order of the sites follows the increasing distance to the edge.

TABLE 2

Mean position of the population of important linyphiid and lycosid species and their numbers in the adjacent areas.

Species	Forest	Edge	Position	Total numbers
Oedothorax apicatus	1	4	46.01	1339
Oedothorax fucsus	0	0	46.00	67
Bathyphantes gracilis	2	15	22.90	250
Lepthyphantes tenuis	9	22	10.60	77
Erigone atra	14	44	30.45	1594
Erigone dentipalpis	2	1	31.89	254
Meioneta rurestris	2	2	35.39	233
Pardosa lugubris	44	107	4.60	280
Pardosa prativaga	6	17	30.69	361
Trochosa ruricola	37	79	11.26	291

DISCUSSION

The importance of nearby habitats for polyphagous predators has been stressed by several studies. Especially the forest ecotone has been the subject of a number of studies that states that they hold a larger numbers of species than the centre of the forest (eg. LUCZAK 1991, BLICK & BLISS 1991, HÄNGGI 1991). Further, some studies have tried to increase numbers of beneficial arthropods by establishing within field stripes (THOMAS *et al.* 1992). These should ease dispersal into the field. However, the question is if the arthropods living in these stripes will penetrate into the field and subsequently establish a population. Studies on carabids shows a positive response to increasing numbers of nearby habitats (THOMAS *et al.*, 1992, COOMBES & SOTHERTON 1986). Several studies on habitat requirements and migration of wolf spiders shows a pattern with a wintering area and a spring migration into adjacent fields. The overwintering habitats of wolf spiders were studied by NØRGAARD (1951), Edgar (1970), EDGAR & LOENEN (1974), and BAYRAM & LUFF (1993). They concluded that grass, and especially grass tussocks, are important shelters in the winter period. The dispersal patterns of lycosids were studied by RICHTER (1970) and VANGSGAARD *et al.* (1990), and DENNIS (1991) concluded that as the aeronautic activity of lycosids are low, their ability to migrate into the field are less than the more aeronautic linyphiids. However, VANGSGAARD *et al.* (1990) showed that the dispersal speed of a population of Pardosa lugubris was 2 meters per day. So small to medium sized fields would be covered within a month.

This study confirms the overall dispersal patterns of the lycosids (fig.5). However, there was some contradictions between this and the other Danish study on the dispersal of *Pardosa lugubris* (VANGSGAARD *et al.* 1990). In the present study it remained close to the field edge and did not penetrate the field centre. The explanation might be that the former study was carried out on a relative small field completely surrounded by forest or that the mixed crop in the studied field created an environment more suitable for *P.lugubris*. In Switzerland HÄNGGI (1991) showed that *P.lugubris* did not penetrate more than a few metre into a meadow from the surrounding forest. In the present study other wolf spider species eg. *P.prativaga* and *Trochosa ruricola* moved into the field, and especially juveniles moved fast into the field. Other *Pardosa* species (*P.palustris*, *P.agrestis*, *P.amentata* (Clerck,1757), *P.monticola* (Clerck,1757), *P.nigriceps* (Thorell,1856), and *P.pullata* (Clerck,1757)) were only found in the field, but this must be explained by their dispersal into the field as juveniles. Identification of juveniles would then be necessary to verify dispersal patterns of these species. However, the overall dispersal patterns of juveniles support the idea of a general dispersal of lycosids into the field.

From mid July a dispersal pattern of lycosids out of the field was seen. This could be explained by the females searching for suitable areas for rearing her offspring. The effect of wolf spider predation on pest species would then be strongest in June and July. However, as NYFFELER & BENZ (1988) stated, the numbers of wolf spiders and their relative low capture rate predicted that the effect on the pest species were of minor importance. Population numbers of wolf spiders are very difficult to

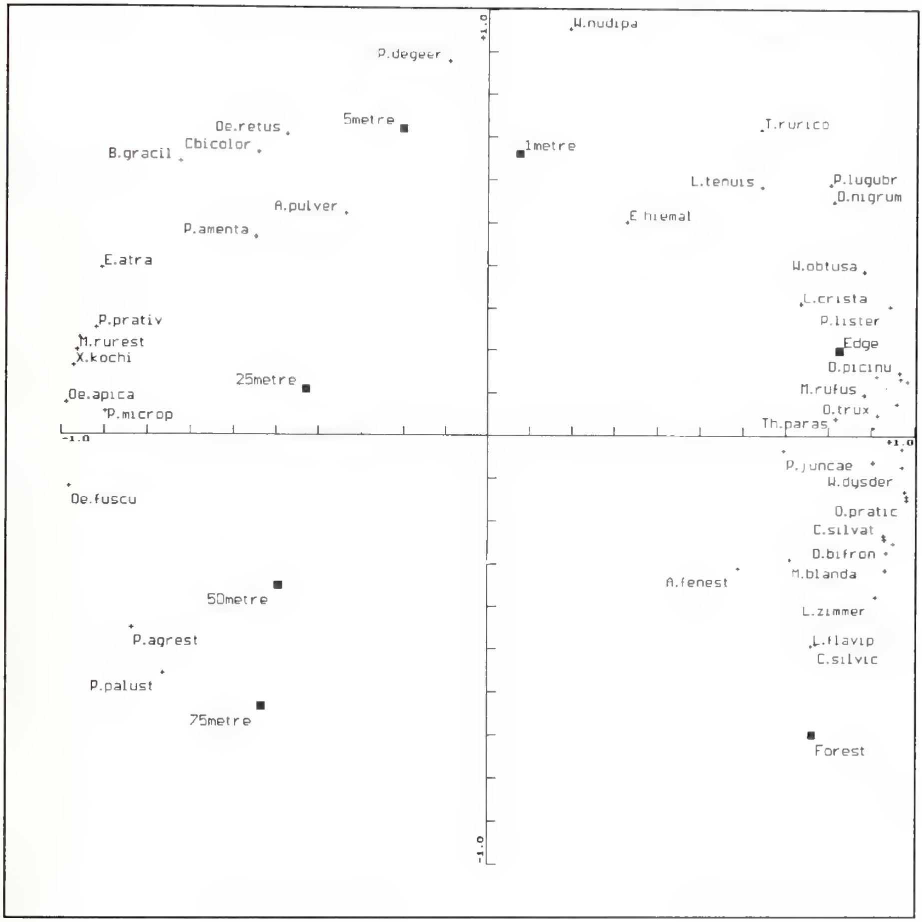


FIG. 5

Principal component analysis of species and sites.

estimate in the field, but probably the maximum densities are between 1 and 10/m2 (NYFFELER & BENZ 1988, SAMU & SAROSPATAKI 1995). These numbers are much lower than the densities of linyphiids with more than 500/m2 at maximum (TOFT *et al.* 1995). Although this wolf spider predation might be well synchronized with the life cycles of aphid species in Danish crops it seems uncapable of controlling the aphid numbers.

It seems evident that lycosids disperse into the field from habitats outside the field, but the question of linyphiid dependence on habitats outside the field is less obvious. Toft et al. (1995) showed that rotation and sowing in spring reduced spider density to less than 10%; so the spider fauna are a mixture of survivors, their off-

spring and spiders dispersing into the field. Although only 3 buckets were used to monitor spider ballooning it gave an indication of that ballooning activity had a minor importance in the distribution of spiders during spring and summer. If we pool all the 1991 data, ballooning activity would give a total precipitation of 3.78 spiders m^{-2}. If the important linyphiids depended on the field edge we would expect to find a dispersal pattern from the grass strip into the field. This was not the case as it seems that throughout the period the numbers of these spiders declined as we move closer to the edge. It is consistent with the finding that only a few of these spiders were caught in the forest and at the grass strip. It seems that some of the species are avoiding the area close to the field edge - at least the inner 5 metres. Especially *Oedothorax apicatus* showed this pattern as only 5 specimens (0.4%) of this species were caught in the forest and at the grass strip. This is supported by the findings of NYFFELER & BREENE (1992) who concluded that densities of *E.atra*, *E.dentipalpis* and *Oe.apicatus* were higher in the centre of a Swiss winter wheat field. This could lead us to the conclusion that increasing the numbers of linyphiids is not obtained by providing more within field habitats of this type. In a further Swiss study HÄNGGI (1991) showed that forest dwelling spider species did not penetrate more than 10 metre into a meadow. In Poland LUCZAK (1991) stated that the forest ecotone acted as a barrier to dispersal into the surrounding fields. However, it seems to be a statement without taking in account the knowledge about the typical spider fauna of field systems. The typical spider species in fields are usually not originating from forest systems but from more open habitats. If the forest ecotone were artificially removed the numbers of spiders from the forest might increase in the adjacent metres of the field. But it would be very risky to predict that these spider species would disperse and establish substantial populations in the centre of the field.

The very common use of pitfall traps have been discussed in several papers (UETZ & UNZICKER 1976, TOPPING & SUNDERLAND 1992, TOPPING 1993, DINTER 1995, TOFT *et al.* 1995, ULBER & WOLF-SCHWERIN 1995, SUNDERLAND *et al.* 1995). They state that results from pitfall catches should be interpreted with cautiousness as numbers caught are a result of several factors. Important factors are density, activity, season, habitat structure, and species differences in respond to the pitfall traps. However, the pitfall traps are usefull in comparing distributional patterns and for studies on phenology and faunistics. In the present study there might be problems in interpreting pitfall catches in the field versus outside the field as the activity of the spiders might be affected by the structural differences between the two habitats.

The ideas of establishing within field habitats for increasing the density of spiders and other polyphagous predators seems to be partly supported by this study. However, this is only evident in lycosids as it was impossible to establish a connection between the linyphiid spider fauna of the field and the surrounding habitats. In Sweden LAGERLÖF & WALLIN (1993) showed that the floristic composition of field margins affected the spider activity significantly. It might be that other types of field margins could increase numbers of linyphiids but the finding that the most important species seems to avoid the forest and grass strip do not look promising. And so far it has not been possible to find any publication of evidence of linyphiids dispersing

from unmanaged habitats to field systems. Although there is no direct dependence of the field edges there might be an indirect effect, eg. the field edges providing prey species in certain critical periods of the season. But still the mechanisms behind the population dynamics between natural and cultivated areas are not sufficiently understood. What we need are detailed studies on population dynamics at species level before we can quantify and model the interactions between the field and the surrounding areas.

SPECIES LIST 1991
AMAUROBIIDAE
Amaurobius fenestralis (Stroem,1768)
DICTYNIDAE
Lathys humilis (Blackwall,1855)
GNAPHOSIDAE
Zelotes subterraneus (C.L.Koch,1833)
Z. lutetianus (L.Koch,1866)
Z. pusillus (C.L.Koch,1833)
MICARIDAE
Micaria pulicaria (Sundevall,1832)
Micaria aenea Thorell
CLUBIONIDAE
Clubiona reclusa O.P.-Cambridge,1863
C. pallidula (Clerck,1757)
C. terrestris Westring,1851
C. compta C.L.Koch,1839
C. diversa O.P.-Cambridge,1862
ZORIDAE
Zora spinimana (Sundewall,1833)
THOMISIDAE
Xysticus cristatus (Clerck,1757)
X. kochi Thorell,1872
X. lanio C.L.Koch,1835
X. ulmi (Hahn,1831)
Ozyptila praticola (C.L.Koch,1837)
O. trux (Blackwall,1846)
PHILODROMIDAE
Thanatus striatus C.L.Koch,1845
LYCOSIDAE
Pardosa agrestis (Westring,1861)
P. purbeckensis F.O.P.-Cambridge,1895
P. monticola (Clerck,1757)
P. palustris (Linnaeus,1758)
P. pullata (Clerck,1757)
P. prativaga (L.koch,1870)
P. amentata (Clerck,1757)
P. nigriceps (Thorell,1856)
P: lugubris (Walckenaer,1802)
P. paludicola (Clerck,1757)
Alopecosa pulverulenta (Clerck,1757)
Trochosa ruricola (Degeer,1778)
T. terricola Thorell,1856
PISAURIDAE
Pisaura mirabilis (Clerck,1757)
AGELENIDAE
Circurina circur (Fabricius,1793)
Cryphaeca silvicola (C.L.Koch,1834)
HAHNIIDAE
Hahnia montana (Blackwall,1841)
Mimetidae
Ero furcata (Villers,1789)
THENIDIIDAE
Crustulina guttata (Wider,1834)
Theridion sisyphium (Clerck,1757)
T. bimaculatum (Linnaeus,1767)
Robertus lividus (Blackwall,1836)
R. neglectus (O.P.-Cambridge,1871)
Enoplognatha ovata (Clerck,1757)
E. thoracica (Hahn,1833)
TETRAGNATHIDAE
Pachygnatha clercki Sundevall,1823
P. listeri Sundevall,1830
P. degeeri Sundevall,1830
LINYPHIIDAE
Ceratinella brevipes (Westring,1851)
C. brevis (Wider,1834)
Walckenaeria acuminata Blackwall,1833
W. alticeps (Denis,1952)
W. cucullata (C.L.koch,1836)
W. dysderoides (Wider,1834)
W. nudipalpis (Westring,1851)
W. obtusa Blackwall,1836
W. atrotibialis (O.P. Cambridge,1878)
W. unicornis (O.P.-Cambridge,1861)
Entelecara acuminata (Wider,1834)
Dicymbium nigrum f. *brevisetosum* Locket,1962
D. tibiale (Blackwall,1836)
Gongylidium rufipes (Sundewall,1829)
Dismodicus bifrons (Blackwall,1841)
Gonatium rubens (Blackwall,1833)
G. rubellum (Blackwall,1841)
Maso sundewalli (Westring,1851)
Pocadicnemis juncae Locket & Millidge,1953
Oedothorax fuscus (Blackwall,1834)
O. retusus (Westring,1851)
O. apicatus (Blackwall,1850)
Pelecopsis radicicola (L.Koch,1872)
Cnephalocotes obscurus (Blackwall,1834)

Troxochrus scabricolus (Westring,1851)
Minyriolus pusillus (Wider,1834)
Tapinocyba pallens (O.P.-Cambridge,1872)
Thyreostenius parasiticus (Westring,1851)
Monocephalus carstaneipes (Blackwall,1834)
Mioxena blanda (Simon,1884)
Saloca diceros (O.P.-Cambridge,1871)
Gongylidiellum vivum (O.P.-Cambridge,1875)
Micrargus herbigradus (Blackwall,1844)
M. apertus (O.P.-Cambridge,1871)
Erigonella hiemalis (Blackwall,1841)
Savignia frontata (Blackwall,1833)
Diplocephalus latifrons (O.P.Cambridge,1863)
D. picinus (Blackwall,1841)
Araeoncus humilis (Blackwall,1841)
Erigone dentipalpis (Wider,1834)
E. atra Blackwall,1833
E. longipalpis (Sundevall,1830)
Porrhomma microphthalmum (O.P.-Cambridge,1871)
Porrhomma lativela Tretzel
P. egeria Simon,1884
P. montanum Jackson,1913
Agyneta sp.
Meioneta rurestris (C.L.Koch,1836)
M. viaria (Blackwall,1841)
Centromerus sylvaticus (Blackwall,1841)
Centromerus dilutus (O.P.-Cambridge,1871)
C. incilium (L.Koch,1881)
Centromerus sp.
Tallusia experta (O.P.-Cambridge,1871)
Centromerita bicolor (Blackwall,1833)
Saaristo abnormis (Blackwall,1841)
Macragus rufus (Wider,1834)
Bathyphantes gracilis (Blackwall,1841)
B. nigrinus (Westring,1851)
Diplostyla concolor (Wider,1834)
Lepthyphantes alacris (Blackwall,1853)
L. tenuis (Blackwall,1852)
L. zimmermanni Bertkau,1890
L. cristatus (Menge,1866)
L. mengei Kulczynski,1887
L. flavipes (Blackwall,1854)
L. tenebricola (Blackwall,1854)
L. ericaeus (Blackwall,1853)
L. pallidus (O.P.-Cambridge,1871)
L. insignis (O.P.-Cambridge,1913)
L. angulatus (O.P.-Cambridge,1881)
Neriene clathrata (Sundewall,1830)
Linyphia hortensis Sundewall,1830
Microlinyphia pusilla (Sundewall,1829)

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Spinnengemeinschaften auf einem typischen Ackerbaustandort Mitteldeutschlands und deren Beeinflussung durch unterschiedliche Pflanzenschutzintensitäten im Verlauf einer Fruchtfolgerotation (Spinnen in Agroökosystemen)

Christa VOLKMAR
Martin-Luther-Universität Halle-Wittenberg, Landwirtschaftliche Fakultät, Institut für Pflanzenzüchtung und Pflanzenschutz, Ludwig-Wucherer-Str. 2, D-06099 Halle/Saale, Germany.

Spider populations on a typical field site in Central Germany and special influences of various plant protection intensities during a crop rotation sequence. - On the 43 ha field the crop sequence included winter barley, maize and winter wheat. For this purpose 6 plots sized 72 x 200 m each were established. On two control plots no plant protection measures were applied. Another two were intensively treated with pesticides. On two plots purposeful plant protection measures were practised with consideration of the threshold values. The epigeous spiders were sampled by using 9 pitfall traps.

The activity density of the spider populations in winter barley was determined in the winter season. The 1826 spiders belonged to 32 species of 12 families. In maize 11 045 spiders were identified in the test period (May to September, 1992). Herbicidal treatments in May and June did not directly influence the activity density of the spiders. However, reproduction rate and thus total numbers were evidently affected, especially in the dominating species. In winter wheat (1993) the control variants revealed the highest activities ($\bar{x}$ 2,81 *O. apicatus* per day and trap). There was no statistical difference to the variant with targeted treatment ($\bar{x}$ 2,68 *O. apicatus* per day and trap). In the intensive treatments $\bar{x}$ 1,83 *O. apicatus* animals per day and trap were counted. The dominating Linyphiidae were represented by 29 species. Altogether 70 species from 14 families were recorded.

Key-words: spiders - pitfall traps - winter barley - maize - winter wheat - side effects of pesticides - supervised plant protection

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EINLEITUNG

Spinnen prägen ganzjährig das Faunenbild der Bodenoberfläche mitteleuropäischer Agroökosysteme (GEILER 1963; LUCZAK 1979; NYFFELER & BENZ 1987). Ihre artliche und quantitative Zusammensetzung wird dabei weniger von der Pflanzenart als vielmehr vom Bodentyp und dessen Feuchtigkeits- und Wärmequalitäten bestimmt (HEYDEMANN & MEYER 1983). Da den räuberisch lebenden Araneae bei der Regulation von Schädlingspopulationen eine große Bedeutung zugesprochen wird, war es Anliegen dieses Beitrages zu prüfen, wie die epigäische Begleitfauna in ihrer Zusammensetzung und ihrer Aktivitätsdichte auf unterschiedliche Pflanzenschutzmaßnahmen auf einem typischen mitteldeutschen Ackerbaustandort reagiert.

MATERIAL UND METHODEN

Die Freilanduntersuchungen wurden in den Jahren 1991 bis 1993 auf einem Standort (Barnstädt, Kreis Querfurt) im mitteldeutschen Trockengebiet durchgeführt. Dieser Agrarraum ist durch das Vorherrschen ertragsreicher Schwarzerdeböden (Bodenform: Lößtieflehm) gekennzeichnet, wobei die relativ geringen jährlichen Niederschläge in erster Linie ertragsbegrenzend wirken (1992: 576 mm, 1993: 572 mm).

Auf einem 43 ha großen Feld untersuchten wir die Fruchtfolge Wintergerste (Umbruch Frühjahr 1992 infolge Trockenheit), Mais und Winterweizen. Dazu wurden 6 Parzellen von jeweils 72 x 200 m Größe angelegt. Auf zwei Kontrollen (V_2, V_5) unterblieb jeglicher Pflanzenschutz, 2 Parzellen (V_1, V_4) wurden intensiv mit Herbiziden, Fungiziden und Insektiziden behandelt, während in den anderen beiden Feldbereichen (V_3, V_6) ein gezielter Pflanzenschutz unter Beachtung von Schwellenwerten praktiziert wurde. Zur Erfassung der epigäischen Spinnenfauna dienten jeweils 9 Bodenfallen pro Parzelle. Im Winterhalbjahr 1991/92 registrierten wir an 9 Leerungsterminen (10.10.1991–23.4.1992) die Aktivitätsdichte der Spinnenpopulation. Infolge der Herbsttrockenheit lief die Wintergerste erst sehr spät und unregelmäßig auf, so daß keine Pflanzenschutzmittel zum Einsatz kamen.

Im Mais erstreckte sich die Fangperiode vom 14.5.1992–14.9.1992 (14 Leerungstermine). Es wurden folgende chemische Behandlungen durchgeführt. Am 21.5.1992 die Unkrautbekämpfung in den Intensivvarianten 1 und 4 mit Stentan-Pack (2,8 l/ha Gardoprim, 1,7 l/ha Stomp Sc) und am 30.6.1992 mit Basta (3,0 l/ha Glufosinate). Am 1.6.1992 erfolgte in den Varianten 3 und 6 eine gezielte Spritzung mit Buctril (1,5 l/ha Bromoxynil). In den unbehandelten Kontrollparzellen verunkrautete der Mais sehr stark durch *Chenopodium* und *Amaranthus*-Arten.

Der Winterweizen wurde 1993 zwischen dem 20.4.1993 und 3.8.1993 beprobt (16 Leerungstermine). Folgende Präparate kamen zum Einsatz. In den Intensivvarianten neben dem Herbizid Duplosan KV (DC 28), die Fungizide Sportak Alpha und Corgan-Pack zu DC 32 sowie Simbo (DC 39) und Sambarin (DC 65). Weiterhin wurde das Insektizid Decis (DC 39 und DC 60) gespritzt. In den gezielt behandelten Parzellen war nur die Applikation der Fungizide Sportak Alpha (DC 32) und Sambarin (DC 65) erforderlich.

ERGEBNISSE

Wintergerste–Winteraspekt

Die insgesamt 1826 Spinnen waren 32 Arten aus 12 Familien zuzuordnen (Tab. 1). An allen Kontrollterminen traten Spinnen in den Fallen auf, wobei die Linyphiidae mit > 90% der Population dominierten (19 Arten). Die Artenliste der Linyphiidae (Tab. 2) weist einige winteraktive Arten aus, die in Fängen während der Vegetationsperiode nicht auftraten (*Centromerus sylvaticus*, *Mioxena blanda*, *Centromerita bicolor*). Für die gesamte Fangperiode ermittelten wir eine durchschnittliche Aktivitätsdichte von 0,16 Spinnen pro Tag und Falle, dabei war eine gleichmäßige Verteilung zwischen den geplanten Varianten festzustellen.

TAB. 1

Übersicht über die auf einem Wintergerstenfeld bei Barnstädt gefangenen Spinnen (Araneae).

Familie	Anzahl
Linyphiidae	1654
Thomisidae	56
Tetragnathidae	42
Theridiidae	24
Lycosidae	16
Gnaphosidae	14
Araneidae	12
Philodromidae	2
Clubionidae	2
Pisauridae	2
Agelenidae	1
Liocranidae	1
Summe	1826

Mais–Sommeraspekt

Im Kontrollzeitraum fingen sich in den 54 Bodenfallen 11 045 Spinnen. Die 34 Arten konnten 10 Familien zugeordnet werden, wobei die Linyphiiden mit 22 Arten am häufigsten auftraten. Einen Überblick über die am häufigsten gefangenen epigäischen Spinnen gibt Tab. 3. Anhand der eudominanten Art *Oedothorax apicatus* wird beispielhaft der Einfluß unterschiedlicher Pflanzenschutzintensitäten auf das Aktivitätsverhalten analysiert (Abb. 1). *Oedothorax apicatus* zeigte bis Mitte Juni nur eine geringe Aktivität im Maisbestand. Am 29.6.92 registrierten wir in allen drei Intensitätsstufen (i: 0,39; g: 1,03; K: 1,49 *O. apicatus* pro Tag und Falle) ein erstes Maximum. Die stärkere Aktivität der Männchen (2449 Tiere) gegenüber den Weibchen (1488 Tiere) läßt sich als Beginn der Fortpflanzungsperiode interpretieren. Nach diesem Kontrolltermin konnte in allen Varianten ein Rückgang der Aktivitätsdichte beobachtet werden, welcher in den behandelten Varianten deutlicher als in der Kontrolle ausfiel. Im September kam es zu einem nochmaligen Anstieg der Aktivitätsdichten. Bei Betrachtung des gesamten Untersuchungszeitraumes zeigten

TAB. 2

Artenliste der Linyphiidae (Araneae) ermittelt auf einem Wintergerstenfeld in Barnstädt

Araeoncus humilis (Blackwall)
Bathyphantes gracilis (Blackwall)
Centromerus sylvaticus (Blackwall)
Centromerita bicolor (Blackwall)
Diplostyla concolor (Wider)
Erigone atra (Blackwall)
Erigone dentipalpis (Wider)
Erigonella hiemalis (Blackwall)
Lepthyphantes mengei Kulczynski
Lepthyphantes tenuis (Blackwall)
Meioneta rurestris (C.L. Koch)
Mioxena blanda (Simon)
Oedothorax apicatus (Blackwall)
Ostearius melanopygius (O. P.-Cambridge)
Pocadicnemis juncea Locket & Millidge
Porrhomma microphthalmum (O. P.-Cambridge)
Tapinocyboides pygmaeus (Menge)
Tiso vagans (Blackwall)
Walckenaeria corniculans (O. P.-Cambridge)

TAB. 3

Übersicht über die Anzahl gefangener epigäischer Spinnen auf einem Maisfeld in Barnstädt 1992 (i - Intensivbehandlung, K - kein Pflanzenschutz, g - Schadschwellenkonzept)

Art/Familie Linyphiidae	V_1, V_4 i	V_2, V_5 K	V_3, V_6 g
Oedothorax apicatus	734	1963	1240
Erigone atra	570	1020	507
Erigone dentipalpis	313	900	345
Lepthyphantes tenuis-Gruppe	76	92	89
Meioneta rurestris	220	254	310
Porrhomma microphthalmum	207	179	172
Juvenile	217	377	207

sich in den Kontrollparzellen die höchsten Werte der Aktivität ($\bar{x}$ 0,83 *O. apicatus* pro Tag und Falle), gefolgt von der gezielt ($\bar{x}$ 0,52 *O. apicatus* pro Tag und Falle) und der intensiv behandelten Variante ($\bar{x}$ 0,30 *O. apicatus* pro Tag und Falle). Der Anteil der Männchen an der Gesamtpopulation betrug 62%. Zusammenfassend läßt sich feststellen, daß die Herbizidbehandlungen im Mai und Juni nur eine schwach aktive Spinnenpopulation trafen. Eine direkte Beeinflussung der räuberisch lebenden Spinnen war bei Aktivitätsdichten unter einem Tier pro Tag und Falle nicht nachweisbar. Eine Beeinflussung der Araneen durch die Herbizide lag nur mittelbar vor, auf die unterschiedliche Verunkrautung der Varianten reagierten die Arten mit ihren spezifischen ökologischen Ansprüchen verschieden.

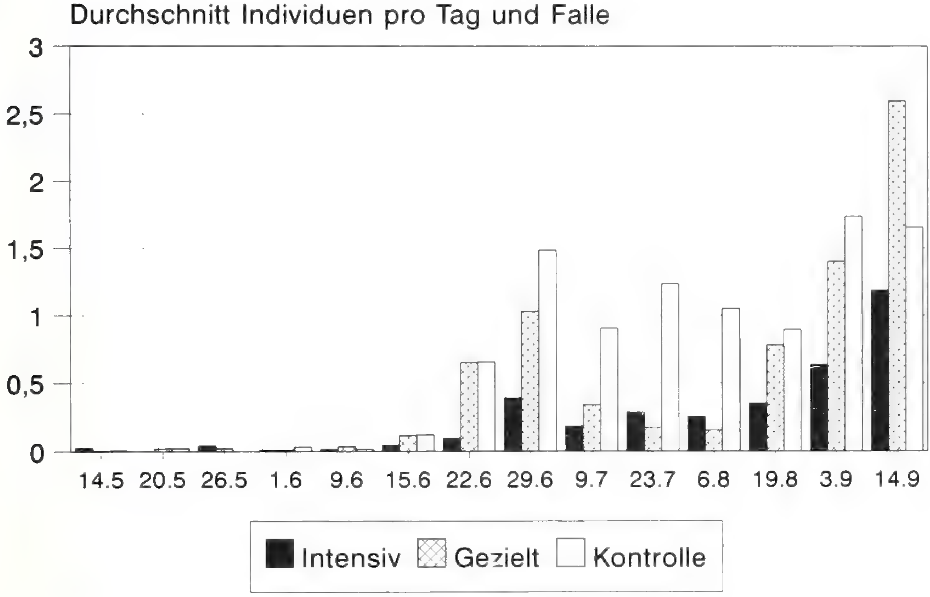

FIG. 1

Oedothorax apicatus (Blackwall), Mais 1992

Winterweizen–Sommeraspekt

Im Überwachungszeitraum (20.4.93–3.8.93) fingen sich in den 54 Bodenfallen insgesamt 22 167 Spinnen. Die 70 Arten waren 14 Familien zuzuordnen, wobei mit 29 Arten die Linyphiidae dominierten. Einen Überblick über die Anzahl ausgewählter Arten der epigäischen Spinnenfauna vermittelt Tab. 4. Anhand der eudominant auftretenden Linyphiidae *Oedothorax apicatus* wird eine Beurteilung der Spinnenpopulation in den einzelnen Varianten vorgenommen (Abb. 2). Während des Zeitraums der chemischen Behandlungen lag die Aktivitätsdichte in allen Teilstücken im Bereich < 1 Spinne pro Tag und Falle. Zu einem Anstieg der Dichtewerte kam es Ende Juni, Anfang Juli, wobei in den Kontrollen am 29.6.93 ($\bar{x}$ 7,63 *O. apicatus* pro Tag und Falle) die meisten Spinnen nachzuweisen waren. In den intensiv gespritzten Parzellen zeigte sich ein verändertes Aktivitätsverhalten. Die Maximalwerte wurden erst verzögert am 27.7.93 erreicht und lagen mit Werten von $\bar{x}$ 5,78 *O. apicatus* pro Tag und Falle unter denen von Kontrolle und gezielt behandelten Varianten. Bei Betrachtung der gesamten Fangperiode zeigte sich, daß bei einer gezielten Spritzung nach Schadschwellen ähnlich hohe Aktivitätsdichten (gezielt: $\bar{x}$ 2,68 *O. apicatus* pro Tag und Falle) wie in den unbehandelten Feldteilen ($\bar{x}$ 2,81 *O. apicatus* pro Tag und Falle) erreicht wurden. Der mehrfache Einsatz von Pflanzenschutzmitteln führte zu einem deutlichen Rückgang der Aktivitätsdichten ($\bar{x}$ 1,83 *O. apicatus* pro Tag und Falle).

TAB. 4

Übersicht über die Anzahl gefangener epigäischer Spinnen auf einem Winterweizenfeld in Barnstädt 1993 (i - Intensivbehandlung, K - kein Pflanzenschutz, g - Schadschwellenkonzept)

Art/Familie Linyphiidae	V_1, V_4 i	V_2, V_5 K	V_3, V_6 g
Oedothorax apicatus	3657	5255	5279
Erigone atra	593	1293	972
Erigone dentipalpis	233	503	501
Meioneta rurestris	329	332	347
Porrhomma microphthalmum	102	52	73
Araeoncus humilis	38	31	37
Lepthyphantes tenuis-Gruppe	89	28	64
Lycosidae	35	220	21
Pardosa agrestis	61	keine Art-	51
Pardosa prativaga	50	bestimmung	70

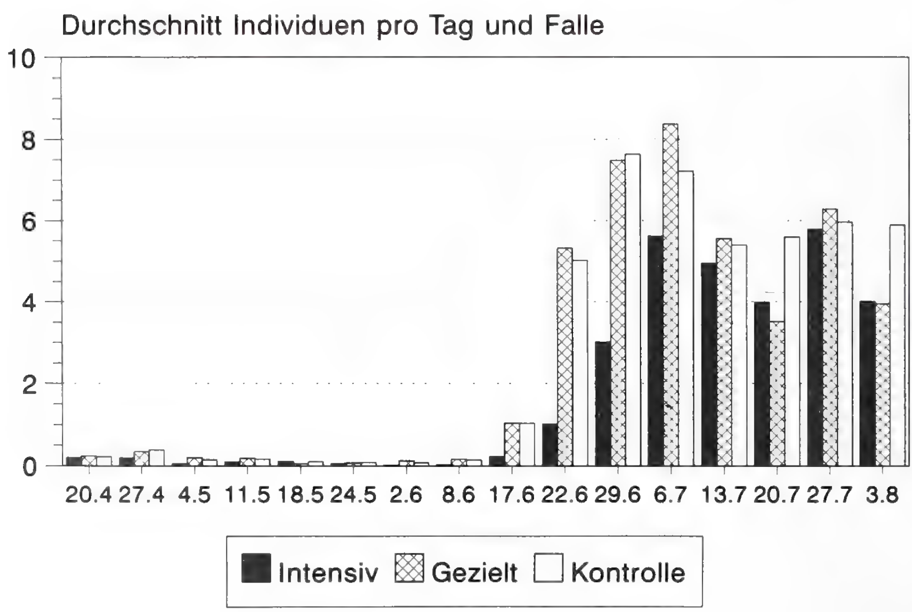

FIG. 2

Oedothorax apicatus (Blackwall), Winterweizen 1993

DISKUSSION

Bei Betrachtung des Winteraspekts hinsichtlich Artenspektrum und Dominanzverhältnis auf einem Wintergerstenfeld bei Halle erwiesen sich die Linyphiiden mit mehr als 90% der adulten Tiere als eindeutig dominierende Familie. Von den 19 Linyphiidenarten waren am häufigsten die ganzjährig aktiven Spezies *Erigone atra*, *Erigone dentipalpis* und *Meioneta rurestris* nachzuweisen. Diese Ergebnisse decken sich gut mit Resultaten, die von GEILER (1963) für Sachsen und THALER & STEINER (1975) für Niederösterreich veröffentlicht wurden.

Während der Vegetationsperiode von Mais und Winterweizen war die Linyphiidae *Oedothorax apicatus* die häufigste Art. Sie erreichte fast durchgängig in allen Varianten Aktivitätsdominanzen, die sie als eudominante Spezies auswiesen, ein Befund, der bereits von BEYER (1981) und VOLKMAR *et al.* (1994) für das mitteldeutsche Trockengebiet beschrieben wurde. Weiterhin zeigt eine Auswertung von Veröffentlichungen zur Spinnenfauna aus den Bundesländern Sachsen und Sachsen-Anhalt (GEILER 1963; BEYER 1981; LÜBKE-AL HUSSEIN & WETZEL 1993; VOLKMAR & UHLEMANN 1995), daß hinsichtlich der Artenzahl und Individuen- bzw. Aktivitätsdichte seit den 50ziger Jahren keine langfristigen Veränderungen im Faunenbild der Bodenoberfläche von Feldern zu beobachten waren. Besonders die an den offenen Lebensraum gut angepaßten Feldarten (*Oedothorax apicatus*, *Erigone atra*, *Erigone dentipalpis*, *Meioneta rurestris*, *Porrhomma microphthalmum*, *Pardosa agrestis*, *Pardosa prativaga*) erreichten in den Kontrollparzellen und gezielt behandelten Feldteilen hohe Zahlenwerte. Ihre lange Verweildauer auf dem Acker, ihre zeitige Präsens im Frühjahr und ihre prädatorische Leistung machen Spinnen zu interessanten Objekten bei der Erarbeitung von Nutzensschwellen. Die Analyse von Auswirkungen unterschiedlicher Pflanzenschutzintensitäten auf die epigäische Spinnenfauna zeigt deutlich, daß ein intensiver Herbizid-, Fungizid- und Insektizideinsatz die Aktivitätsdichte der dominanten Arten signifikant mindert. Diese Aussagen werden auch durch Untersuchungsergebnisse von ULBER *et al.* (1990) gestützt, der in der Region Hannover in einer Fruchtfolge Winterraps, Winterweizen, Zuckerrübe betriebsüblichen Pflanzenschutz mit einem gezielten Bekämpfungskonzept verglich. Zusammenfassend kann man sagen, daß ein gezielter Einsatz von Pflanzenschutzmitteln unter Beachtung von Schadschwellen geeignet ist, einer beträchtlichen Anzahl von Spinnenarten ihren Lebensraum auf unseren Kulturfeldern zu erhalten.

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The shrub layer spider communities: variation of composition and structure of the gorse clump communities in western France

Frédéric YSNEL, Alain CANARD & Gérard TIBERGHIEN
Laboratoire de Zoologie et d'Ecophysiologie, (U.A. I.N.R.A./C.N.R.S.1853), Université de Rennes I, Campus de Beaulieu, F-35042 Rennes CEDEX, France.

The shrub layer spider communities: variation of composition and structure of the gorse clump communities in western France. - The comparison between the spider communities inhabiting the shrub layers of gorses reflects the constancy of a group of dominant species for several years in a same continental study plot. We observe a substitution in the dominant species among the different functionnal groups when comparing the continental, littoral and insular site communities This has to be related to macroclimate differences between the sites investigated. However, the species composition of the functionnal groups of spiders inhabiting different gorse clumps in a same littoral macroclimate area strongly varies The possible reasons for these variations are suggested.

Key-words: spiders - communities - gorse clumps - islands - western France

INTRODUCTION

This study is part of a general work on western France spider communities. Our investigations on this topic started with the description of functional groups in several heathland plant communities with quantitative results on spatial distribution and densities of species according to their hunting habits (CANARD 1990). In the present paper, we consider more precisely the structure of spider communities of shrub layers of gorse clumps (*Ulex europaeus* Linné, 1758) which typically belong to littoral and continental heathlands in Brittany. Because of their mosaic distribution, we should find a specific spider community in this type of habitat. Climatic conditions strongly vary between continental and coastal areas (LARIVIERE & VERDOU 1969) therefore the spider communities are compared for three types of gorse clumps - a continental type, a littoral type and an insular type.

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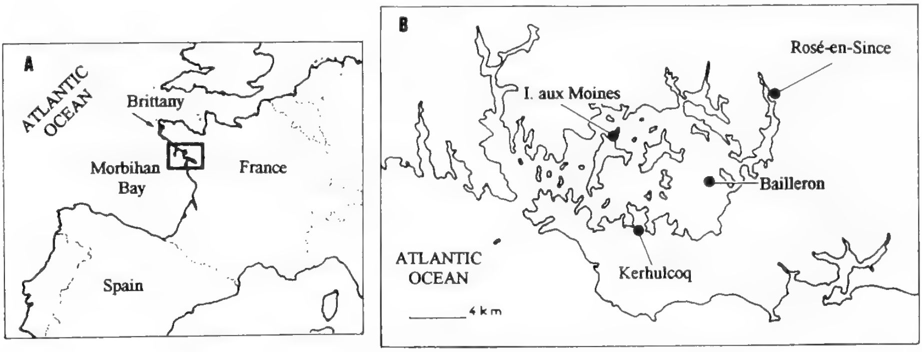
MATERIALS AND METHODS

The continental site lies in central dry heaths of Brittany at 47°58N, 2°53O. The plot was in Baulon and the gorse clumps were investigated during the years 1976-1977, in spring 1980 and in spring 1981 (CANARD 1984). For this site, the spiders were collected once a month by branch beating and branch collecting (CANARD 1984). The littoral and insular gorse clumps were located in the Morbihan Bay in the south of Brittany (about 47°30'N, 3°W) The Morbihan bay forms a great littoral basin scattered with some thirty islands or islets (cf. Map). The bay is characterized by a higher number of sunny days and by a lower number of winter



frosty days than the continental zone because of the inland sea (DENIS 1978). Four sites have been selected in this area; two of them are located on islands (insular sites1, 2): "Ile aux Moines" is one of the biggest island (surface area: 2.74 km^2) and "Ile Bailleron" is one of the smallest (0.05 km^2). These two islands are very close to the continent. The two other sites (littoral site 1: Rosé-en-Since; littoral site 2: Kerhulcoq) are situated along the coast and are fifteen kilometers apart. The gorse clumps investigated in "Ile Bailleron" were less developped (poor vegetation area); However, the three other sites selected in the Morbihan bay exhibit no basic habitat differences (same vegetation height, volume and area). In the Morbihan bay, we only collected the species by branch beating on low and upper gorse layers. The spiders were sampled in june 1995 and the branches were beaten until we collected at least 250 individuals per gorse clump. The comnunities are compared using the Blondel index of communities similarity H'_β (derived from the shannon index) (BLONDEL 1979):

$$H'_\beta = H'_{ab} - 0.5\ (H'_a + H'_b)$$

(where, H'_a, H'_b= Shannon index for communities a and b; H'_{ab} = Shannon index for communities mixed). The nomenclature of spiders used follows PLATNICK (1989). Functional groups of species are established according to their hunting habits (CANARD 1990). In order to simplify the comparisons of the spider communities, table 1 and 2 only refer to species represented by at least 5 individuals. The total list of species is given in annex1.

RESULTS

1) Comparison of spider communities inhabiting gorse clumps between the continental zone and the Morbihan Bay

The global comparison between the continental, littoral and insular plots emphasizes the differences between the three spider communities (table 1 and annex 1). The species diversity is similar on continental (43 sp.) and littoral plots (50 sp.) but remains considerably low on the island plots (27 sp.). Among the total of 82 species collected, a low proportion of common species (30%; 25 species) is found on the three sites. Furthermore, the analysis of species distribution according to functional groups (table 1) clearly indicates a substitution concerning the dominant species among these groups. We can observe for instance a complete substitution of the dominant species for ambush hunters and sheet-weavers between the spider communities of continental and littoral or insular gorse clumps. The frame-web spiders communities are nearly the same on the three sites (except *Theridion pallens*), but in this case, there is a substitution in the dominance of the species. The comparison of continental samples shows that, except for *Lathys humilis*, no differences in the dominant spiders species composition are detected between the data collection of march-april 1980 and those of march-april 1981.

2) Comparison of littoral and insular gorse clumps in the Morbihan Bay

60 species were identified in the Morbihan bay (annex 1). No more than 48% of the species are to be found in two different sampling sites at the same time. This low percentage is a result of the great changes in the composition of the dominant species for each functionnal group between littoral and insular gorse clumps (table 2). The two littoral gorse clumps exhibit the higher percentage of common species while the lowest percentage is observed when comparing the communities of insular and littoral gorses (table 3). However, we observed a high percentage of common species between the littoral site 2 and the insular site 1. These results are confirmed when using the Blondel index of similarity which takes into account both presence and dominance of species in the four sites investigated (table 4). The lowest index between insular and littoral communities, and between insular site 1 and littoral site 2 indicates a higher similarity between these communities.

A comparison in the structure of the spider assemblages is given by the relative abundance of the species in the different sites (figure 2). The first littoral site community is clearly dominated by *D. rudis*, which is paradoxally totaly absent on the other sites. *Enoplognatha g. ovata*, one of the dominant species on the littoral site 2, is very poorly collected on islands. The two insular gorse clump communities are dominated by the same group of species but a substitution in the specific dominance can be underlined. These graphs also indicate that one species predominates over the insular communities; therefore the island gorse spider communities are more unbalanced than the littoral gorse spider communities. This result is confirmed by the lowest value of the Shannon evenness index for insular communities (table 5).

TABLE 1

Relative abundance of species (heavy print numbers indicate the main differences in the functionnal groups; bc = branch collecting; bb = branch beating).

	Continental			littoral	insular
	annual sampling 1976-1977 (bc)	march-april 1980 (bb)	march-april 1981 (bb)	june 1995 (bb)	june 1995 (bb)
Diurnal wanderers					
Ero aphana			0.2	1.3	
Pardosa nigriceps		0.13	0.4	0.93	
Dendryphantes rudis	4.6	8.2	3.1	**11.8**	
Eris nidicolens				**12.2**	**12.8**
Heliophanus tribulosus					2.1
Ambush-hunters					
Philodromus cespitum	5.7	4	6.9		
Xysticus sp.	**11.4**	0.08	1.4		
Xysticus lanio				5.7	**23.5**
Philodromus glaucinus				1.9	1.9
Frame-web spiders					
Theridion pallens	**6.2**	**9.6**	1.2		
Anelosimus vittatus	2.1	0.53	1		0.35
Dictyna letens	3.6	0.13	0.4	1.3	1.4
Theridion varians	1	0.53		3.2	1.4
Theridion bimaculatum			1.4	0.7	
Anelosimus aulicus	**14**	**25.8**	**19.4**	1.3	
Theridion simile	**27**	**18.2**	**36.9**	1.6	
Theridion mystaceum	**6.8**	**15.6**	**13.9**	3.3	0.5
Lathys humilis	8.3	6.5		2.2	2.8
Theridion tinctum		0.1		2.4	**6.7**
Enoplognatha g. ovata		0.1	1.6	**8.2**	
Lathys sexpustulata				0.8	0.7
Sheet-weavers					
Frontinellina frutetorum	0.5	0.3	1.3		
Peponocranium ludicrum	0.5	1	2.5		
Hybocoptus decollatus				2.1	**10.9**
Linyphia triangularis				2.26	
Lepthyphantes tenuis				3.3	0.52
Oedothorax fuscus				2	
Erigone atra				1	0.17
Orb-weavers					
Araniella curcubitina	1	1.9	0.97		
Zygiella sp.				**9.8**	**26.1**
Araneus diadematus	0.5	0.4	0.19	**10.5**	**1.75**
nocturnal wanderers					
Clubiona comta		0.4	1.17	0.53	
Drassodes cupreus				0.8	
total number of individuals	192	748	512	751	570

Furthermore, specific diversity of the communities strongly decrease on islands. This lowest diversity is closely linked to the low number of sheet-web spiders inhabiting islands (table 6).

TABLE 2

Distribution of species recorded in the Morbihan Bay according to functionnal groups

	Morbihan bay			
	littoral 1	**littoral 2**	**insular 1**	**insular 2**
Diurnal wanderers				
Dendryphantes rudis	**21.1**			
Pardosa nigriceps	1.7			
Ero aphana	1.2	1.5		
Anyphaena accentuata	1.7	0.3	0.4	
Ballus chalybeius	0.7			1.25
Eris nidicolens	6.5	19.4	17	10.4
Heliophanus tribulosus			2	2.2
Ambush-hunters				
Philodromus glaucinus	0.23	3.9	4	0.3
Xysticus lanio	5	6.7	**36**	**13.5**
Frame-web spiders				
Theridion bimaculatum	**0.9**	**0.3**		
Theridion simile	**1.7**	**1.5**		
Anelosimus aulicus	**1.4**	**1.2**		
Lathys sexpustulata	1.4		1.6	
Enoplognatha g. ovata	**3.8**	**14**	0.4	
Theridion mystaceum	2.4	4.6	1.2	
Theridion varians	3.3	3	3.2	
Lathys humilis	3.5	0.6	3.6	2.1
Theridion tinctum	3.8	0.6	2.4	**10.1**
Dyctina latens	1.2	2.4	2.4	
Anelosimus vittatus			**0.4**	**0.3**
Sheet-weavers				
Linyphia triangularis	**4**			
Bathyphantes gracilis	0.47	0.6		
Oedothorax fuscus	3.3	0.3		
Lephtyphantes tenuis	1.6	5.5		0.9
Hybocoptus decollatus	1.9	2.4	6.7	**14.2**
Orb-weavers				
Araneus diadematus	**10.4**	**10.6**	2.4	1.2
Zygiella sp.	7.6	12.8	12.2	**37.2**
Nuctenea umbratica		0.6	0.8	2.2
nocturnal wanderers				
Drassodes cupreus	1.4			
total number of individuals	422	329	253	317

TABLE 3

Percentage of common species between the different plots

	littoral 2	insular 1	insular 2
littoral 1	48%	37.8%	22%
littoral 2	/	44.7%	22.2%
insular 1	/	/	35.5%

TABLE 4

Blondel index of communities similarity

	littoral 2	insular 1	insular 2
littoral 1	0.15	0.19	0.24
littoral 2	/	0.09	0.27
insular 1	/	/	0.11

TABLE 5

Shannon index for the different plots

	littoral		insular	
	1 (Rosé-en-Since)	2 (Kerhulcop)	1 (île aux Moines)	2 (Bailleron)
Shannon diversity index (H')	1.22	1.13	0.92	0.78
Shannon evennness index (J')	0.76	0.74	0.69	0.59

TABLE 6

Number of species according to functionnal group for the different sites
(percentages are given in parentheses)

	continental	littoral		insular	
	Baulon	1	2	1	2
Orb-web spiders	7 (16.2)	6 (15.4)	5 (14.7)	4 (19)	7 (33.3)
Frame-webs spiders	13 (30.2)	11 (28.2)	9 (26.4)	8 (38.1)	5 (23.8)
Sheet-webs spiders	6 (14)	10 (25.6)	8 (23.5)	2 (9.5)	2 (9.5)
Ambush hunters	6 (14)	3 (7.7)	4 (11.8)	2 (9.5)	3 (14.3)
Diurnal wanderers	8 (18.6)	7 (18)	4 (11.8)	4 (19)	4 (19)
Nocturnal wanderers	3 (7)	2 (5.1)	4 (11.8)	1 (4.8)	/
total	43	39	34	21	21

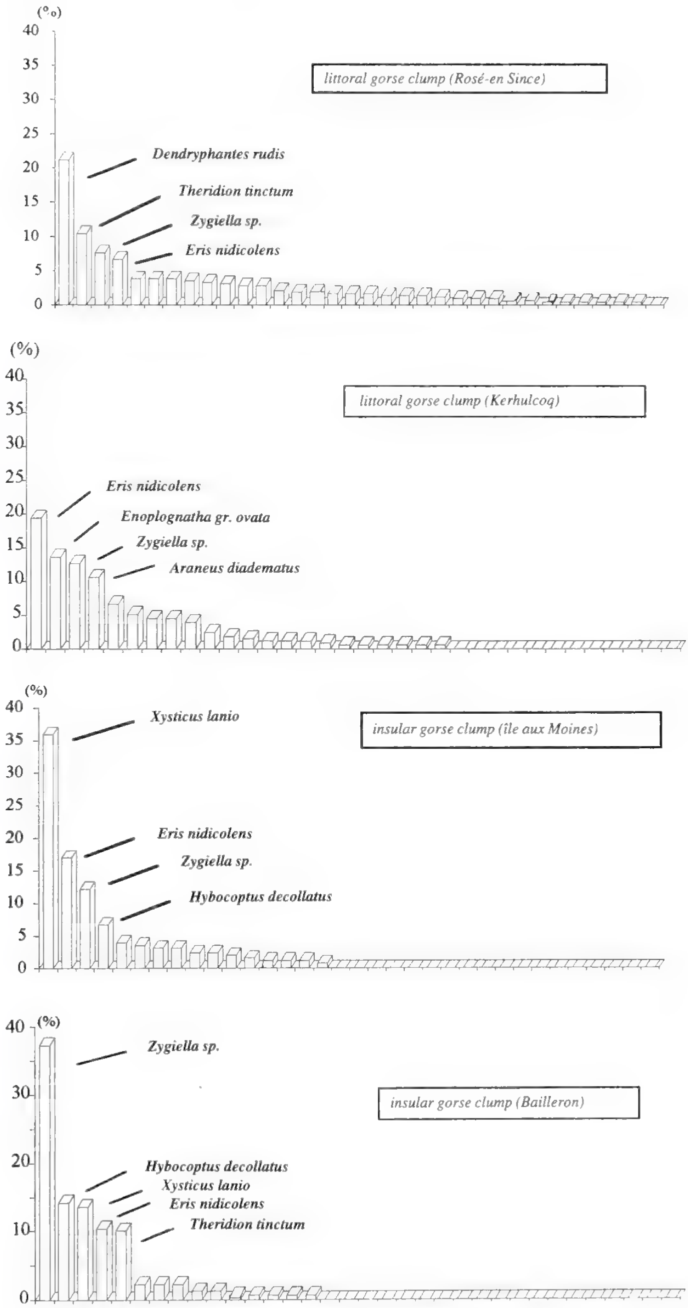


FIG. 2

Relative abundance of the species for the four plots in the Morbihan Bay.

DISCUSSION

This first approach leads to the conclusion that the shrub layer spider communities of gorse clumps vary between continental, littoral and insular sites. Concerning the continental plots, the relative abundance of dominant species can fluctuate from one year to another year, but we can observe a constancy in the presence of these species for 5 years. Numerous other species are also recorded on the gorse clumps but their presence can vary depending on the sampling collection. Most of them are probably typical species inhabiting gorse clumps but they may be underestimated from one sample to the next because of their low density. Among this group, some spiders can also be considered as a guild of "accessory colonizers" and their presence may be dependent on periodically exchange with adjacent zones. There are no considreable variations between the species composition of the "spring community" and the composition of the "annual community" for successive years. This reflects the stability of the spider community of gorse clumps and allows us to compare different communities on the base of the analysis of the spring communities.

Continental and littoral/insular spider communities of gorse clumps strongly differ. These differences are most likely to reflect macroclimate variations between the sites. These climate modifications clearly appear in the species composition of the functional groups. This has to be related to the ecological valence of the species. Evidence of the influence of the warmer macroclimate in the Morbihan Bay is given by the presence of *Eris midicolens*, *Philodromus glaucinus* and *Lathys sexpustulata* which are typical species of France meridional ecosystems. Concerning the insular plots, the scarcity of suitable and adjacent habitats, the lack of some potential preys and the increase of competition are the well known factors usually evocated to explain the lower species diversity (MAC ARTHUR & WILSON 1967; WISE 1993). This study shows a decrease in the number of sheet-weaving species inhabiting islands. Because more than 70% of the spider colonist of shrubs may arrived by aerials means (EHMAN 1993) and because sheet-weavers are the most frequent balloning dispersers (DECAE 1987), one can expect that insular gorse clumps have to be easily colonized by sheet-weavers. In a previous paper (CANARD 1989), we found that the species richness of sheet-weavers in meditteranean zones was low in comparison to temperate zones (where the climate and potential preys are different). The unexpected low number of Linyphiids species on islands could be a result of a difference in macroclimate and/or potential preys between insular and littoral plots. Furthermore, the absence of *D. rudis* and the predominance of the more thermophilous species *E. nidicolens* in the insular diurnal wanderers functionnal group could confirm these suggestions. The comparison between the two littoral spider communities also reveals the absence of the predominant species *D. rudis* on one of the gorse clump. Moreover, a high similarity index is found between this littoral spider community and one of the insular community. This suggests that a difference in microclimate at the shrub layer level occurs between the two littoral zones (this is also suggested because there is no basic differences in the vegetation structure and volume between the two habitats). A previous study demonstrated that the variations in the microclimatic conditions linked

to a variation in the vegetation cover of two similar sites can lead to a change in the species diversity and dominance of ground layer spider communities (CANARD 1990). Although small changes in the spider colonization can occur in relation with the specific structure of each gorse clump, these results obviously suggests that shrub layers spiders communities seems also dependent on microclimatic conditions. Furthermore unpublished observations induce us to suggest that the species composition and the species dominance of continental spider communities of gorse clumps are less exposed to fluctuations than littoral ones because of the most uniformous macroclimate of continental areas. Further studies on other sites are now needed to confirm these hypothesis.

ANNEX 1

Total list of species with numbers of individuals collected in all the sites.

	Continental (43 sp.) annual sampling 1976 -1977	march-april 1980	march-april 1981	littoral (50 sp.) june 1995	insular (27 sp.) june 1995
total number	*192*	*748*	*512*	*751*	*570*
Dominant species					
Philodromus cespitum	11	30	35		
Theridion pallens	12	72	6		
Xysticus sp.	22	6	7		
Anelosimus aulicus	27	193	99	10	
Theridion mystaceum	13	117	71	25	3
Lathys humilis	16	49		17	16
Dendryphantes rudis	9	62	16	89	
Encoplognatha g.ovata		1	8	62	
Theridion simile	52	136	189	12	
Araneus diadematus	1	3	1	79	10
Eris nidicolens				92	73
Hybocoptus decollatus				16	62
Theridion tinctum		1		18	38
Xysticus lanio				43	134
Zygiella sp.				74	149
others species					
Anelosimus vittatus	4	4	5		2
Araneus angulatus	1				2
Ballus chalybeius		1		3	4
Cheiracanthium sp.			1	1	
Clubiona comta		3	6	4	
Dictyna latens	7	1	2	10	8
Ero aphana			1	10	
Heliophanus cupreus	1	3	2	3	
Mangora acalypha		2	1	2	
Pardosa nigriceps		1	2	7	
Salticus scenicus		1			1
Theridion bimaculatum			7	5	
Theridion varians	2	4		24	8
Anyphanena accentuata				8	
Araniella curcubitina	2	14	5		
Ceratinella brevipes			2		
Clubiona sp.		4	3		
Crustulina sp.			1		
Drassodes sp.	3	1	2		
Dictyna arundinacea	1	10	1		
Frontinellina frutetorum	1	2	7		
Hahnia sp.	1				
Meta sp.		1			
Misumena vatia		2			
Neoscona adianta			3		
Peponocranium ludicrum	1	8	13		
Philodromus rufus		4	3		
Phlegra fasciata	1				

Pisaura mirabilis		1			
Tetragnatha sp.	1	2			
Theridion blackwalli		3	4		
Tiso vagans		1			
Xysticus tortuosus	2				
Linyphiides indeter.	1	4	10		
Agyneta subtilis				2	
Bathyphantes gracilis				4	
Clubiona neglecta				2	
Drassodes cupreus				6	
Dysdera crocota				3	
Erigone vagans				2	
Euophrys erratica				2	
Gibbaranea gibbosa				1	
Gongylidiellum vivum				1	
Hypomma bituberculatum				1	
Linyphia triangularis				17	
Milleriana inerrans				1	
Nigma puella				1	
Meta mengei				1	
Oedothorax fuscus				15	
Ozyptila praticola				1	
Ozyptila simplex				1	
Pachygnatha clercki				1	
Pocadicnemis pumila				1	
Tetragnatha montana				1	
Tibellus sp.				1	
Erigone atra				8	1
Lathys sexpustulata				6	4
Leptyphantes tenuis				25	3
Nuctenea umbratica				2	9
Philodromus glaucinus				14	11
Philodromus dispar				1	2
indetermined (immatures)				16	3
Achaearanea simulans					1
Dipoena melanogaster					2
Episinus sp.					1
Tetragnatha pinicola					1
Heliophanus tribulosus					12
Zilla diodia					1
Hyptiotes sp.					2

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Bulolia, a new genus of Salticidae (Arachnida: Araneae) from Papua New Guinea

Marek ZABKA
Zaklad Zoologii WSRP, PL-08-110 Siedlce, Poland

Bulolia, **a new genus of Salticidae (Arachnida: Araneae) from Papua New Guinea.** - *Bulolia* gen. nov. and two new species: *B. ocellata* (type species) and *B. excentrica* are described from tropical rain forests of Papua New Guinea. The diagnostic characters of the genus are given and its relationship is discussed.

Key-words: *Bulolia* - *B. ocellata* - *B. excentrica* - taxonomy - new genus - new species - Papua New Guinea - rain forest.

INTRODUCTION

The spider family Salticidae comprises some 4500 described species and is world-wide in distribution. Although it presents huge morphological variety of body shapes, sizes, colours, genitalic pattern and living strategies, it has one character in common. The eyes are usually arranged in three rows, possess a complex structure and are capable of acute vision (LAND 1985). In two groups, Lyssomaninae and Athamae, and in some other unrelated taxa (e.g. *Viciria*, *Orthrus*, *Mantisatta*, *Synemosyna*) (PRÓSZYŃSKI 1968; WANLESS 1980*a-c*, CUTLER 1985; CUTLER & WANLESS 1973) the eyes form an additional fourth row. In the case of Lyssomaninae the structure of the copulatory organs and some aspects of behaviour suggest "primitive" status for the group while the position of the Athamae seems derived within the fissident salticids. It is obvious that three or four rows of eyes and their size variation may well occur both in the "primitive" or "derived" salticids and may differ even between closely related genera. On the other hand, the similarities in morphology of legs, chelicerae and genitalia in various unrelated salticid groups is quite often (ZABKA 1990, 1991, 1995).

The methods of specimen examination are routine and described elsewhere (ZABKA 1990). The specimens are deposited in the Queensland Museum, Brisbane (QMB).

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Abbreviations used: QMB - Queensland Museum, Brisbane, AEW - anterior eyes width, AL - abdomen length, CL - cephalothorax length, EFL - eye field length, PEW - posterior eyes width, measurements in mm.

Bulolia gen. n.

Type species: *Bulolia ocellata* sp. n.

Etymology: The name is derived from the locality, Bulolo River area (Papua New Guinea, Morobe Province) and is feminine in gender.

Diagnosis. Medium sized (5–6 mm) spiders. The eyes arranged in four rows. Thoracic slope distinctive, anterior legs long and strong, embolus twisted, seminal reservoir meandering, bulbus without posterior lobe, tibia with single retrolateral apophysis or with additional prolateral process. In comparison to similar (related?) *Athamas* the spiders larger, abdomen more elongated and anterior legs relatively longer.

Relationships. The shape of the cephalothorax and the structure of the palpal organ of the genus *Bulolia* show similarities to the genus *Athamas* (Figs 17–19). Both possess distinctive thoracic slope, meandering seminal reservoir and twisted embolus. The most obvious difference is in the structure of the anterior legs: relatively delicate in *Athamas* and strong and elongated in *Bulolia*. Also cheliceral dentition is slightly different, being fissident in *Athamas* and intermediate in *Bulolia*. Discussing the relationships of "lower" and "true" salticids, WANLESS (1980*c*) pointed out that the eyes may differ in size and in arrangement both in distant and related taxa (Figs 17, 20, 22, 24, 26). Thus it seems reasonable to hypothesise that similar eye arrangement present in jumping spider may well be a "primitive" (Lyssomaninae) or a "derived" (Athamae) character. Also the genitalic structure in Salticidae is of limited use, being simple and similar even in different sections and subfamilies (ZABKA 1995).

Bulolia ocellata sp. n. (Figs 1–3, 9–10)

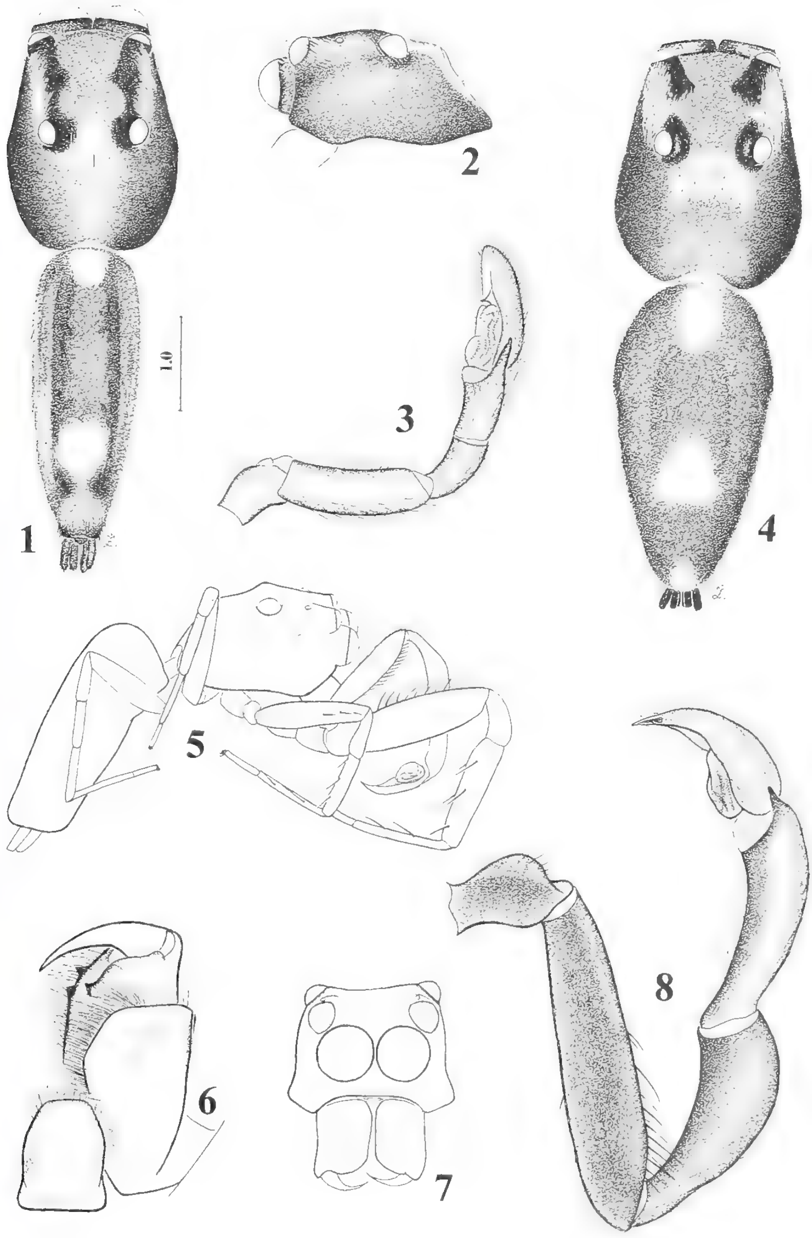
Material: Male holotype, Papua New Guinea: Central Province, Varirata National Park, rain forest, 24 Aug. 1985, leg. D.J. Court, QMB.

Diagnosis. Abdomen with two spots of white hairs, palpal patella and tibia neither elongated nor swollen, cymbium not pointed, prolateral tibial apophysis missing. Stridulating spines on femur of pedipalps and first legs absent.

Description. Cephalothorax dark-orange, darkening towards lower margins, lighter on eye field. Eye surrounding darker. Fovea region and eye field sides with numerous white hairs. Abdomen elongated, centrally greyish-brown with two spots of white hairs and with lighter terminal part, sides lighter with greyish coating. Spinnerets grey-brown. Clypeus and chelicerae orange-brown, the latter lighter apically. Maxillae and labium dark-orange, sternum yellow, venter grey. Legs I long, honey-orange, ventrally, dorsally and distally yellowish-orange. Other legs yellow, more delicate. Leg formula: 1–4–2–3.

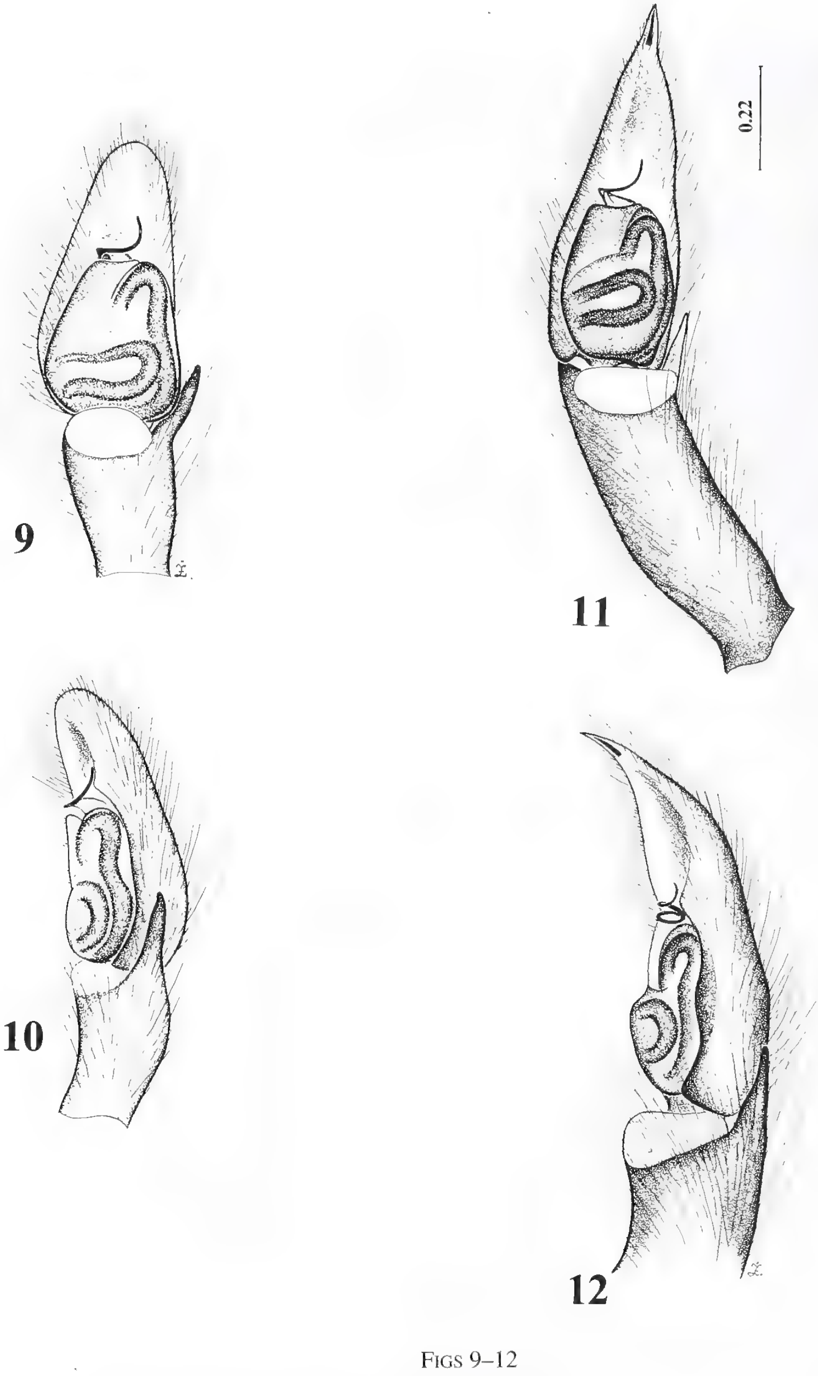
Palpal organ as illustrated in Figs 3, 9–10.

Dimensions: CL 2.15, EFL 1.20, AEW 1.25, PEW 1.20, AL 3.00.



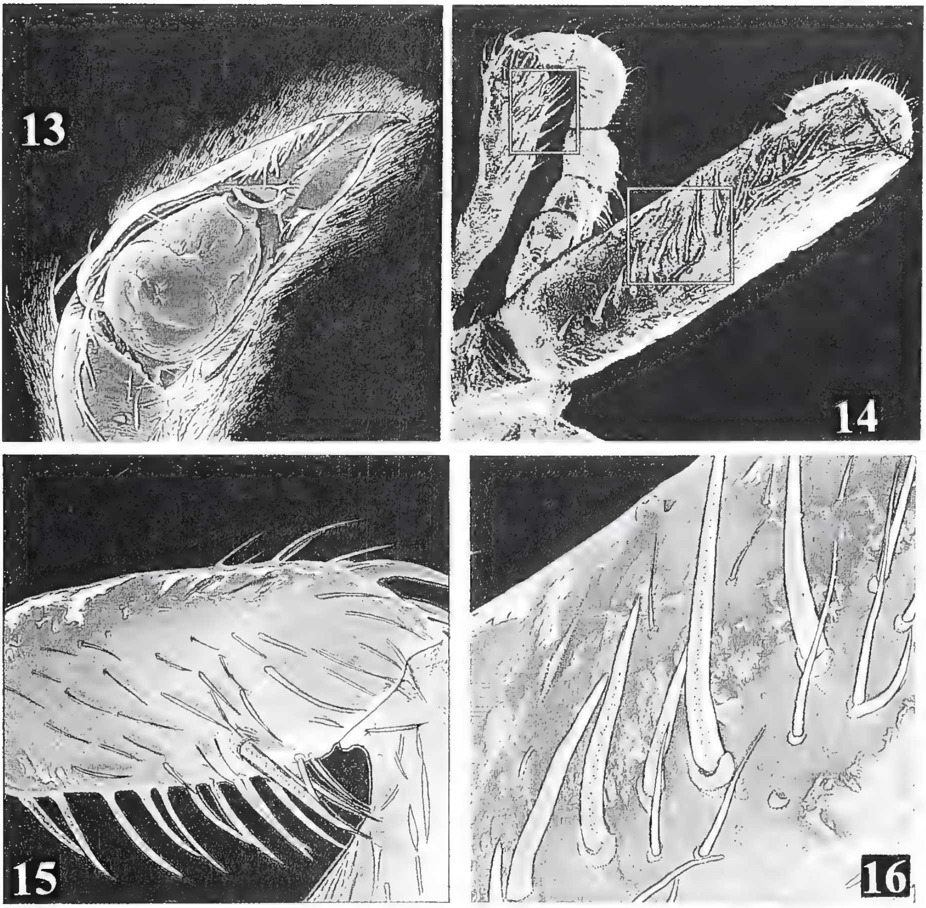
FIGS 1–8

Bulolia ocellata sp. n.: dorsal aspect (1), lateral view of cephalothorax (2), pedipalp (3). *Bulolia excentrica* sp. n.: dorsal aspect (4), lateral view of the body (5), cheliceral dentition (6), frontal aspect (7) and pedipalp (8).



Figs 9–12

Palpal organ of *Bulolia ocellata* (9, 10) and *Bulolia excentrica* sp. n. (11, 12).



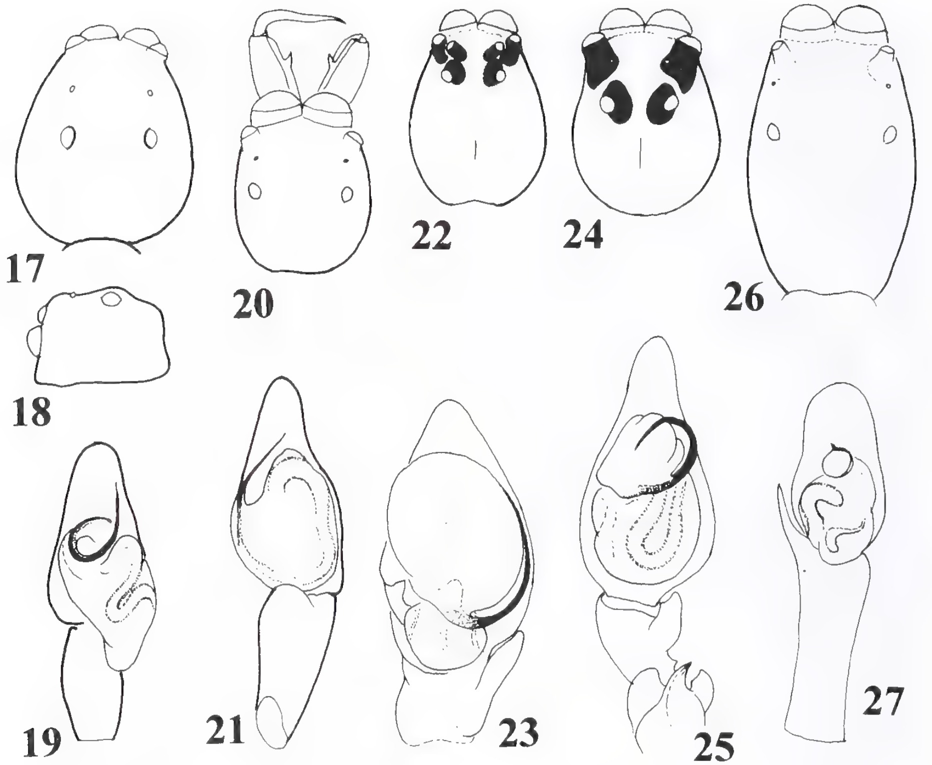
Figs 13–16

Bulolia excentrica sp. n.: palpal organ (13), femoral spines on pedipalp and leg I(14), femoral spination on the pedipalp (15) and femoral spines on leg I(16).

Bulolia excentrica sp. n. (Figs 4–8, 11–16)

Material: Male holotype, Papua New Guinea: Central Province, Varirata National Park, rain forest, 2 June 1985, D.J. Court, QMB; male paratype, Morobe Province, Bulolo River area, J.B. McAdam National Park, lower mountain forest, 900 m., on *Araucaria* trunk, 10 July 1988, D.J. Court, M. Zabka, QMB.

Diagnosis. Abdomen with three dorsal light spots. Pedipalps strongly elongated, patella and tibia swollen, the latter with additional prolateral apophysis, cymbium pointed. Femora of pedipalps and first legs with rows of (stridulatory?) spines (Figs 14–16).



FIGS 17–27

Eye arrangement and genitalic pattern in various unrelated genera: *Athamas* (17–19); *Orthrus* (20, 21), *Asemonea* (22, 23), *Pandisus* (24, 25); *Mantisatta* (26, 27). Drawings from CUTLER & WANLESS (1973), WANLESS (1980*b*, *c*), JENDRZEJEWSKA (1995).

Description. Cephalothorax orange-brown, slightly darkening towards the lower margins, eye surroundings darker. The sides of eye field and fovea region covered with numerous white hairs. Abdomen elongated, its central part light-brown with three spots of white hairs. Laterally abdomen greyish with lighter spots, spinnerets darker. Clypeus brown, chelicerae (Fig. 6) lighter, especially in apical parts. Maxillae (Fig. 6) elongated, dark-orange with small darker spots. Labium brown. Sternum rather wide, yellow with orange margin. Venter grey-brown. Legs I massive and long, brown, their dorsal and ventral parts yellow-orange. Femora with a row of spines (Fig. 16). Other legs shorter and more delicate, yellowish. Leg formula: 1–4–2–3.

Palpal organ shown in Figs 8, 11–13, palpal femur with strong spines (Fig. 15).

Dimensions: CL 2.35, EFL 1.30, AEW 1.15, PEW 1.25, AL 3.25.

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Early stages of orb web construction in *Araneus diadematus* Clerck

Samuel ZSCHOKKE
Department of Zoology, South Parks Road, Oxford, OX1 3PS, England
and
Zoologisches Institut, Rheinsprung 9, CH-4051 Basel, Switzerland

Early stages of orb web construction in *Araneus diadematus* Clerck. - The early stages of orb web construction are the least studied and the most poorly understood, because the behaviour of the spider at that stage lacks the repetitiveness of later stages, the timing is unpredictable and the moves of the spider cannot be deduced from the finished web.
In the present study, all moves of the spider during web construction were recorded using computerised image analysis. The early stages of web construction of several webs were then reconstructed from these recordings and analysed in detail.
The construction leading to the proto-hub was found to be highly variable. It was also found that during its construction, the spider employs a series of fixed behavioural patterns in seemingly random order. These patterns are 'designed' in a way to make it very likely that a proto-hub will emerge. Once the spider had established this proto-hub, its behaviour became more stereotyped and predictable.
The costs to explore a new site were estimated by measuring the distance walked by the spider. These costs were compared to the costs of adapting the framework of an existing web and it was found that re-building and existing web costs much less compared to building a web from scratch.

Key-words: Spider - Web - Construction - Behaviour - Behavioural pattern - Exploration - Behavioural costs - Animal tracking

INTRODUCTION

Many of us have watched with fascination how a spider builds the web, or at least how it builds the spirals and with a little bit of luck on our side, one could also follow the construction of the radii. You need much more than that little bit of luck to

Current address: Institut für Natur-, Landschafts- und Umweltschutz, Universität Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland.

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watch construction from the very start, since the time of the onset of the construction is unpredictable (WITT *et al.* 1968); and even those who were lucky enough to be present when the first threads were laid had problems in actually describing it when they saw it for the first time (EBERHARD 1990), since the spider acts in a seemingly random fashion. Always laying down a new thread (the dragline), it is busy moving and removing threads laid previously until suddenly the proto-hub emerges (MAYER 1952). This proto-hub is then moved to its final position and the construction of the frame threads and the radii starts.

Many published descriptions of the early stages of construction are – as EBERHARD (1990) put it – "probably simply wrong or flawed in ignoring variations". EBERHARD's own description of the early stages of web construction by *Philoponella vicina*, *Leucauge mariana*, and *Nephila clavipes* is very thorough, but hard to understand for the non-specialist and therefore not suitable for publication in popular publications; and it is in these articles where most of the 'simply wrong' descriptions can be found (e.g. CROMPTON 1950, LEVI 1978).

The present paper aims to remedy this situation by depicting the web construction process in, hopefully, an understandable but yet essentially correct way. It also attempts to describe some mechanisms the spider may employ to start a new web. I shall argue that there is no fixed pattern the spider employs to do so, it rather uses one of several possible rules all designed to advance the construction to the point where a knot with several radial lines has emerged. This not may then be used as a proto-hub. The process of building a new web from scratch has not been optimised by natural selection for two reasons. It would not be possible for the spider to rely on a fixed behavioural pattern – as it does for the construction of the rest of the web – since the environment is highly variable and the spider therefore has to react in a flexible manner. In addition, since spiders usually build several webs at the same site, re-using the framework of the previous web, they do not have to build a web from scratch very often.

Along with the description of the early stages of web construction I was also interested in its costs. Since absolute costs are very hard to measure, I attempted to compare the costs of the exploration stage between webs built on supporting structures of different complexity and to compare the exploration costs to the costs of rebuilding an existing web. To get an idea of the order of magnitude of these costs they were also compared to the costs of the rest of the web construction.

MATERIALS AND METHODS

The position of the spider during web construction was monitored continuously with a video camera and an image scanner HVS VP112. The position of the spider was then transferred to a Macintosh computer which recorded the subsequent positions of the spider. For a more detailed description of the method see (ZSCHOKKE 1994). This procedure produced a detailed account of all moves of the spider, but it did not record the positions of the threads. Repeated recordings of the spiders' moves during web construction made it possible to single out spiders that readily built webs.

I managed to video-tape the web construction (from the very beginning) of three webs built by three different spiders. The observations made from studying the thread positions in these recordings – together with pictures of the finished webs – allowed me later to reconstruct the thread positions of some of the other webs of which I had only recorded the moves, giving me a total of 9 recordings with known thread positions.

The spiders used in this study were immature male and female *Araneus diadematus* of similar size, habituated to the laboratory environment (16L/8D, 50% rH, 25°C). They built webs on U– shaped frames (Fig. 1), 18 cm high and 16 cm wide. Each time they had built a web, they were fed with one or two fruit flies Drosophila sp. and the web was sprinkled liberally with water. The web was then removed, the frame wiped clean of remaining silk and the spider re-released onto the right hand stick and the recording was restarted.

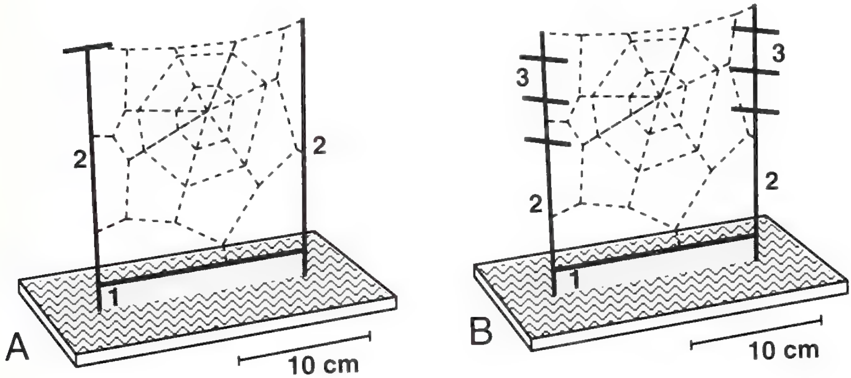

FIG. 1

Supporting structures for the web construction of the spiders. The structures consisted of a perspex plate (1) placed vertically in a tray of water (to prevent escape of spider). On both sides of that plate a transparent drinking straw (2) was fixed with one or several cross-bars (3). Two structures of different complexity were used in this study: a simple one (A) with one cross-bar parallel to the perspex plate and a complex one with six cross-bars (B) turned 45° out of the plane of the perspex plate. The spider was always released on the top of the stick on the right hand side.

From the recordings of the moves of the spider I inferred the positions of the threads. To better visualise the continuity of the web construction process, I divided the web construction into small steps, extracted for each step the moves of the spider from the recordings and added the position of the threads and the frame in different colours (similar to the frames shown in Fig. 2). This gave me a sequence of pictures which I then joined in a Macintosh computer into a QuickTime® movie, allowing me to study the construction of the webs repeatedly.

Laboratory measurements of exploration distance

Following EBERHARD (1972), the exploration stage (or web removal stage) of the web construction was defined as anything the spider did before it moved the proto-hub.

The costs of exploring a new site were assessed by measuring the distances the spider had walked during the exploration stage. I assumed that the distance the spider had covered was proportional to the energy expenditure of the spider; since the spider always leaves a dragline, the distance covered is the roughly the same as the length of silk produced; the distance covered is also roughly proportional to the locomotory energy used by the spider.

The costs of exploring a new site versus removal of an existing web were assessed by comparing the distances the spiders covered to do these tasks. On the simple supporting structure (Fig. 1A) 37 webs built by 6 different spiders were recorded, and on the complex supporting structure (Fig. 1B) 38 webs built by 5 different spiders. On four occasions I (but not the observing computer) missed the completion of a web and the spider proceeded in due course to remove this web and construct a new one on the same supporting structure. In three out of these four cases, the spider removed the web and proceeded with the construction of the second one without further exploration; in the fourth case, the spider's track after removal of the first web looked similar to tracks typical for the exploration stage, and this web was therefore not used in the analysis.

The distance the spider had covered during the exploration stage was first compared between spiders on the same supporting structure using a Kruskal-Wallis test. Since this comparison gave no differences between spiders (simple supporting structure: $p=0.466$, complex supporting structure: $p=0.340$) and since I have good reasons to believe that the spiders did not learn from one web construction to the next (ZSCHOKKE 1994, see also Fig. 4), the webs of all spiders were pooled for each supporting structure.

I compared the distances the spiders had covered for the removal of a web before building a second one with the exploration distances for both supporting structures. I also compared the exploration distances between the two supporting structures using the Mann Whitney U-test. In addition, I compared the distances for the rest of the web construction.

RESULTS

Description of orb web construction in the laboratory

Bridging the open gap

As a first step, the spider bridges the open space between the two sticks. In the laboratory (where there is no wind) this is done by attaching the dragline at the top of one stick and then walking the detour along the bottom of the supporting structure (Fig. 2A). When it reaches the other stick, it climbs up, sometimes only partly, to a

point where it tightens and attaches the dragline to use it to cross back to the top of the first stick (PETERS 1989).

The spider then usually tries to establish a thread as high up as possible; this may be achieved by replacing the original thread or by adding another one (Fig. 2B). During these early steps of web construction, the spider may pause at any time, sometimes for a few minutes, sometimes for several hours.

Establishment of proto-hub and construction of the proto-radii

The spider now establishes the so-called proto-hub, a structure where several threads (the proto-radii) fastened to the supporting structure come together at a single point (Figs. 2C-2E). The establishment of the proto-hub with the construction of the proto-radii is a highly variable process. At first, no pattern can be discovered in the way the spider walks around, constantly laying new threads and sometimes moving or removing older threads. Gradually one point emerges where several proto-radii meet. The spider then continues by constructing a few more proto-radii.

The construction of the proto-radii itself is also highly variable. Most (31 out of 34) proto-radii constructions followed one of six variants of the same basic pattern which is fairly similar to that of the normal radius construction. The spider starts at the proto-hub; then it attaches the dragline at or near the proto-hub. Next it somehow reaches the supporting structure where it attaches the dragline, thus forming the provisional proto-radius. The spider may reach the supporting structure in one of three different ways: it either walks along existing threads (Fig. 2D); or it drops down vertically using the dragline (Fig. 2E); or it uses what I am tempted to call the Tarzan method: the spider – after having attached the thread – walks (usually towards the hub, if the dragline is not originally attached at the hub) a few centimetres and then drops down, swinging around the place where the dragline is attached. When the spider – in full swing – hits another thread or a part of the supporting structure it grabs it and continues the construction from there. Either way, the spider will then return along the provisional proto-radius (reeling it up along the way) back to the hub, inserting the definite proto-radius at the same time.

The spider sometimes performs most of a construction pattern for a proto-radius, but fails to attach a thread when reaching the supporting structure. I could not detect any regularity in the order of the variants used to construct the proto-radii (the variants are distinguished by the place where the provisional radius is attached (at the hub or near the hub) and how the spider reaches the supporting structure).

When the spider has established this proto-hub – usually with four to seven proto-radii (PETRUSEWICZOWA 1938, MAYER 1952, KRIEGER 1992) – it will continue (from now on usually without long rests) by building the first frame thread along the top of the future web. During the construction of the top frame thread, the spider always tightened it whilst sitting in the middle of the top frame thread itself, which seems impractical, since the spider has to lift itself up as well when doing so. It is not known why it does not do it from either end, where the force required would be much smaller. I can only speculate that this position may give the spider better control.

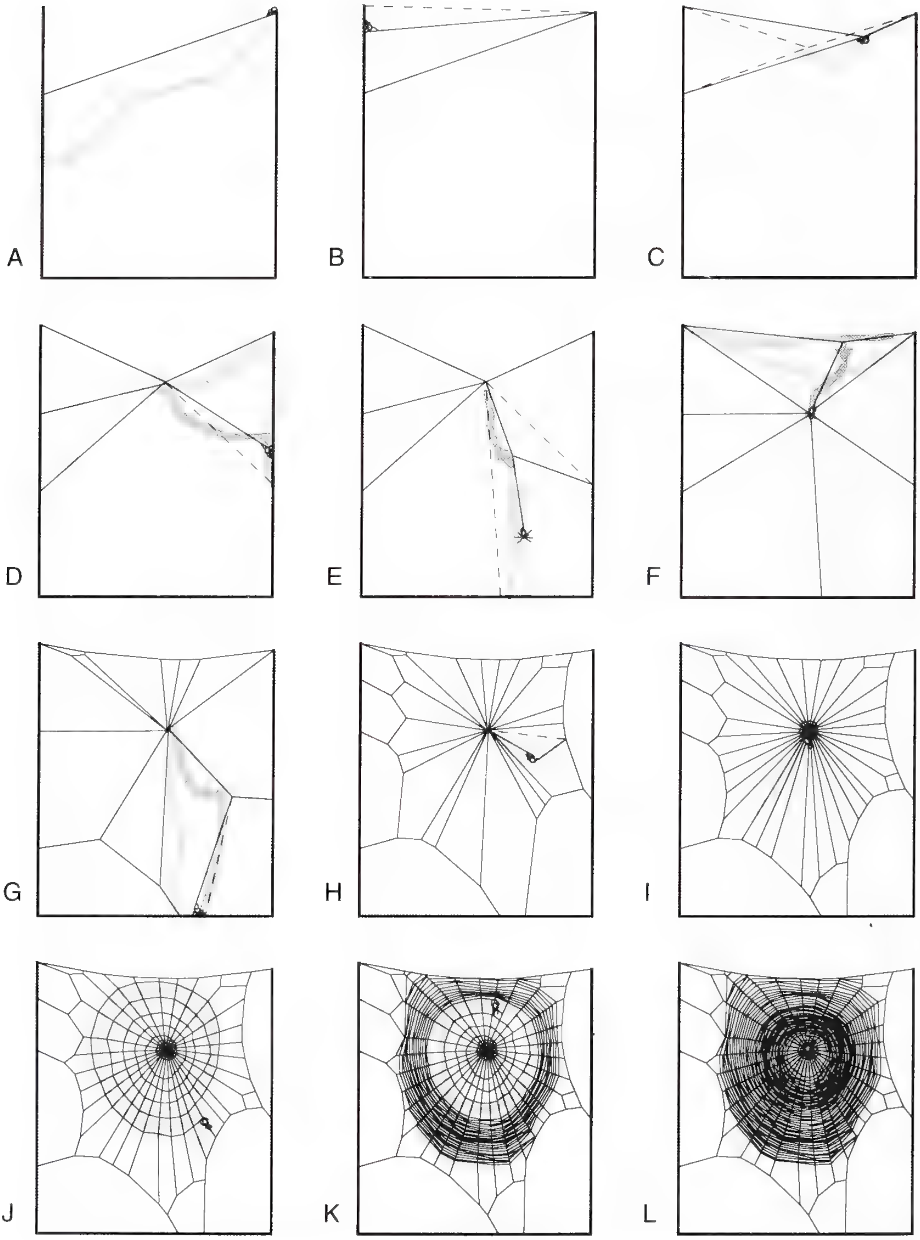

FIG. 2

Outline of orb web construction of *Araneus diadematus* in the laboratory. The drawings are based on recorded moves of the spider, with the threads reconstructed from those moves. It is a slightly simplified account of a web construction selected for its simplicity; early stages (i.e. the

This is immediately followed by moving the proto-hub to its final position, thus turning it into the hub. At the same time the first definitive radius (always between top frame thread and hub) is constructed (Fig. 2F). When the spider has moved the hub it sometimes replaces some of the radii (often only partly), probably to re-adjust their tensions.

Construction of frame and radii

The next stage in the web-building is the construction of the frame and the radii. Primary frame threads (i.e. those attached to anchor threads, MAYER 1952) and secondary frame threads (i.e. those attached to other frame threads) are built using the basic pattern shown in Fig. 2G. The spider walks out along an existing 'exit' radius to attach a thread. Dragging this thread behind, it walks back towards the hub and then along the next lower radius where it attaches that thread to form the frame. It then continues along this newly laid thread back to the upper radius and back to the hub. When the spider builds a secondary radius (i.e. a radius constructed without simultaneous construction of a frame thread, Fig. 2H), it walks out along an existing radius to the frame, then down (always) a few steps along the frame where it attaches the dragline (the 'provisional radius'). The spider then clambers back to the hub, reeling up the provisional radius while simultaneously producing the definitive radius. The remains of the provisional radii can be seen in a web under construction as fluffy white balls of silk in the hub of the web.

The order of the radii construction follows certain patterns; the spider always puts in the new radius immediately below an existing one; never above and never with a large gap where it would later on add another radius (PETERS 1937, REED 1969). It tends to build the radii above the hub before those below it (KRIEGER 1992). Additionally, it adds the radii in an order apparently to balance the forces in the hub (McCOOK 1881, KÖNIG 1951, EBERHARD 1981, WIRTH & BARTH 1992).

ones represented in A-E) are highly variable and usually more complicated than the ones shown here (cf. Fig. 4B). In each picture, the moves of the spider are indicated schematically with grey arrows (light grey – earlier moves; dark grey – later moves). The plain lines show the position of the threads when the 'snapshot' was taken, the dashed lines show the position of the threads when the spider had completed the moves shown in the picture (only where the position of the spider shown differs from the final one). To keep the sequence of pictures lucid, all moves of the spider not resulting in new permanent threads have been omitted in this representation. Remember that the spider always leaves a dragline; in A for instance, it first attached the dragline at the top of the right hand stick and walked down and around the bottom of the supporting structure, always trailing this dragline behind. When it had reached about one third of the height of the left hand stick, it tightened and attached that dragline, thus establishing a first thread across the open space (not shown in the figure). Then it proceeded to walk up to two thirds of the height of the stick, attached the dragline again, walked down and used the thread it had just before laid across the open space to go back to the top of the right hand stick, at the same time removing this thread and still (as always) pulling a dragline behind. Having reached the top of the right hand stick, it tightened and attached the dragline again, thus establishing the thread shown in the figure.

The first frame thread is always the one at the top of the future web, the top frame thread; the other frame threads are only laid after moving the hub.

Frame construction follows quite a rigid pattern (ZSCHOKKE & VOLLRATH 1995). In the 9 webs analysed in detail, I observed few secondary frame-threads (8 of 55). Of the 47 primary frames, 19 were built without inserting a new radius at the same time and not as described by CODDINGTON (1986): "*Uloborus walckenaerius* and *Araneus diadematus* both construct a radius each time they construct a frame line".

Construction of the spirals

When the spider builds the radii it keeps circling the hub to find a gap to place the next radius. This circling then continues after the insertion of the last radius, thus forming the hub structure (Fig. 2I). Circling of the hub changes suddenly without interruption into the construction of the auxiliary spiral (Fig. 2J). The spider finally completes the web by building the capture spiral (Fig. 2K) before going to the centre of the web and remaining there motionless, waiting for prey to fly into the web (Fig. 2L).

The spider usually replaces the web every night (WIEHLE 1927). When it stays at the same place it re-uses large parts of the anchor and frame threads, but it replaces all radii and the capture spiral (CARICO 1986). The old web is ingested and the silk recycled.

ORB WEB CONSTRUCTION IN THE FIELD

In a natural environment outdoors bridging an open space (the equivalent of the step shown in Fig. 2A) is usually achieved by letting a thread fly with the wind (TERBY 1867, HINGSTON 1920, WIEHLE 1927, PETERS 1989); this thread may then become entangled on the opposite side of the open space and enables the spider to cross it. In the laboratory, attempts of the spider to let a thread fly were often observed, but almost never produced results, and when they did, it was to my misfortune because it allowed the spider to leave the field of vision of the camera, often enough to build a web just next to it, leaving me with a blank recording of the moves.

In the laboratory, I never observed web construction based on an initial Y-structure as described by PETERS (1939). This may be due to my relatively small supporting structure or – as suggested by MAYER (1952) – due to the use of spiders of different age-classes or due to the limited space available. Outdoors, the webs of *A. diadematus* often span gaps of several metres (WIEHLE 1927, own observations).

DISTANCES WALKED BY SPIDERS TO CONSTRUCT A WEB

The distances the spiders covered during the exploration stage varied greatly (Fig. 3). For the simple supporting structure it lay between 2.79 and 63.21 m (median=5.61 m, MAD (median absolute deviation)= 1.79 m); for the complex supporting structure it lay between 6.55 and 212.53 m (median=27.60 m, MAD=13.35 m). Even the exploration stages of two consecutive web constructions by the same

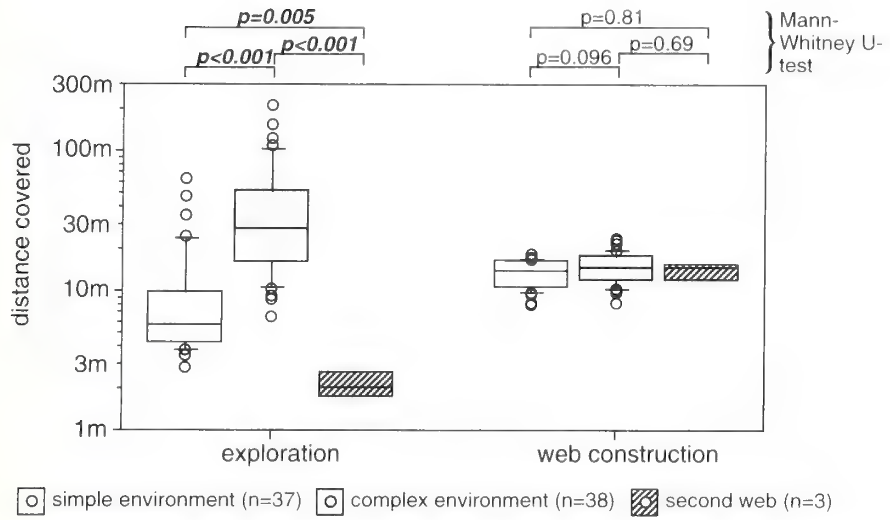

FIG. 3

Box plot of the distances covered by the spider to explore the environment (left) and to build the web (right) on the simple supporting structure (n=37), the complex supporting structure (n=38) and also for second webs (and therefore web removal in the left graph, n=3). The distances were compared using Mann-Whitney U-tests, giving significant ($p<0.01$) p-values between all three groups for the exploring distances but not for the web-building distances.

spider sometimes showed a huge difference (Fig. 4). The distances the spider walked to actually build the web (constructions of radii, auxiliary and capture spiral) varied much less. For webs built on the simple supporting structure they lay between 7.86 and 18.46 m (median=13.64 m, MAD=2.61 m) and for those built on the complex one between 8.24 and 24.09 m (median=14.37 m, MAD=2.72 m).

The distance the spider had moved to remove the old web before constructing a new one (Fig. 3), was significantly smaller than the distance covered to explore the simple supporting structure ($U=1$, $p=0.005$) or to explore the complex supporting structure ($U=0$, $p<0.001$). The distance to explore the simple supporting structure was also smaller than the exploration distance on the complex supporting structure ($U=156$ $p<0.001$). The distances of the actual web construction (Fig. 3) did not differ between the three groups (second web vs. simple: $p=0.81$; second web vs. complex: $p=0.69$; simple vs. complex: $p=0.096$).

DISCUSSION

WEB CONSTRUCTION PATTERNS

I observed large variations in the behaviour of the spiders during the exploration stage of orb web construction. It is not possible for the spider to use a rigid

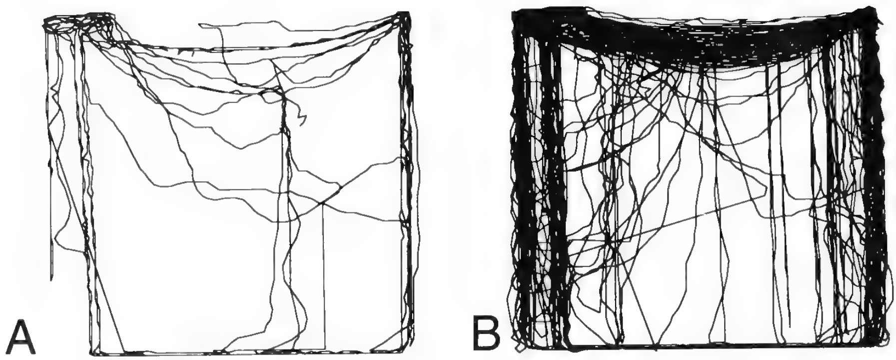

FIG. 4

Recorded tracks of the exploration stage of two consecutive web constructions by the same spider on subsequent days. During the exploration stage of the first web (A), the spider walked 7.28 m and for the second one (B) 63.21 m.

pattern, since the environment is highly variable. With the establishment of the proto-hub with the proto-radii, the spider then laid the foundation for the construction of the rest of the web. This foundation showed less variation and enabled the spider to use a more rigid pattern for the subsequent construction of radii, frame and the spirals. The fact that the spider rested only rarely after the establishment of the proto-hub also indicates the use of a more fixed neural program at this stage.

I had also expected the early stages to be less optimised than later ones, because the spider usually re-uses many anchor threads and frame threads when rebuilding a web (CARICO 1986, WIRTH 1988, own observations). This implies that the early stages of orb construction are not done as often as the later stages and have therefore been under weaker selection pressure.

I have recorded a great number and great variety of web constructions; they however have one flaw in common: they were all recorded in the laboratory. Under natural circumstances, conditions are different; the spider has more space available and it may employ wind currents to establish the first thread. The combination of these two factors certainly influences the behaviour of the spider; to what extent we can only know when detailed and repeated observations have been carried out in the field.

When looking at the results presented in this study, we must remember that most early stages are more complicated than the one presented here (cf. Fig. 4B). The spider often lays threads which serve no apparent purpose and are later removed.

Exploration distance

My analysis of the exploration distances showed clearly that it is much cheaper for the spider to rebuild an existing web rather than building a web at a new site, even when disregarding (as I did in the present study) the risks and costs of moving to and finding a new web-site (Rypstra 1984, Vollrath 1985, Vollrath 1987). The distances travelled for exploring and the distances travelled for building the web were on average about the same. However, the real costs differed, since some of the investment for the actual web building (i.e. the production of the silk) can be recovered when the spider eats the web and thus recycles the silk. I could not observe recycling of silk laid down during exploration.

One aspect of the exploration stage I could not study satisfactorily was how the spider ascertains that the area intended for web construction is indeed free of obstacles. In this study, the spider may have known this after establishing the first thread across the gap; this thread – dragged across the open space – would have been caught by any obstacle if there had been one. Due to the different mechanism of establishing the first thread in nature; the spider may need an additional step to ascertain that nothing interferes with the web to be.

Looking at the overall pattern during the exploration stage, it can be seen that the spider always first established a horizontal thread as high up as possible and then built the web working down from that thread. This automatically ensured an approximately vertical and planar web, at least in my simple environment – but see also (Zschokke & Vollrath in press).

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